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CONTENTS

PAGE

Voice, Courtship, and Territorial Behavior of Ant-Tanagers in British Honduras.....*Edwin Willis* 73

The Nest and Eggs of the Slaty Vireo.....*J. Stuart Rowley* and *Robert T. Orr* 88

Correlation of Variation in the Wrentit with Environmental Gradients.....*Darl E. Bowers* 91

A Blackish Race of the Gray Seedeater of Northern South America.....*Alden H. Miller* 121

Physical Analysis of a Simple Bird Song as Exemplified by the Chipping Sparrow.....*Peter Marler* and *Donald Isaac* 124

FROM FIELD AND STUDY

Changed Status of Several Species of Waterfowl in Alaska.....*Henry A. Hansen* 136

Behavioral and Ecologic Notes on the Brown-headed Cowbird.....*Richard F. Johnston* 137

Occurrence of the Osprey in Uruguay.....*Rodolfo Escalante* 138

Another Record of the Baikal Teal in Northwestern Alaska.....*William J. Maher* 138

Occurrence of Slaty and Dwarf Vireos in Jalisco, México.....*W. J. Schaldach, Jr.* 139

Rare Migrants in Death Valley National Monument, California.....*Roland H. Wauer* 139

Breeding of the Fork-tailed Petrel off the Washington Coast.....*Frank Richardson* 140

An Occurrence of the Rose-breasted Grosbeak in Southern Nevada.....*W. H. Richard* 140

The Rusty Blackbird and Dickcissel in Oregon.....*Ales. Walker* 140

Wilson Petrel off the California Coast.....*I. C. T. Nisbet* and *R. G. McCaskie* 141

Nesting Attempt by a Pair of Barn Swallows in Northern Alaska....*Henry E. Childs, Jr.*, and *William J. Maher* 141

Rocky Mountain Race of the Williamson Sapsucker Wintering in California.....*Ralph J. Raitt, Jr.* 142

NOTES AND NEWS..... 143

THE CONDOR

VOLUME 62 MARCH-APRIL, 1960 NUMBER 2

VOICE, COURTSHIP, AND TERRITORIAL BEHAVIOR OF ANT-TANAGERS IN BRITISH HONDURAS

By EDWIN WILLIS

From February to August, 1957, I studied Red-crowned and Red-throated ant-tanagers (*Habia rubica* and *Habia gutturalis*) at Gallon Jug, British Honduras. This report compares the calls and songs, "courtship," and territorial behavior of these sibling species.

I am indebted to the National Science Foundation for fellowships supporting this study, to the United Fruit Company for transportation to Belize, British Honduras, and to the Belize Estates and Produce Company and the many generous people of that organization for their help in many ways at their camp at Gallon Jug. Peter Marler and the Department of Zoology of the University of California made audiospectrographic equipment available. L. Irby Davis and the Cornell University Library of Natural Sounds provided several ant-tanager recordings for analysis. The American Museum of Natural History and the United States National Museum loaned specimens for examination of crest development and other features. S. M. Russell, P. A. Daigre, and the Museum of Natural Science at Louisiana State University provided mounted specimens for tests. R. J. Newman of that Museum has taken time to examine the manuscript critically; and G. H. Lowery, Jr., directed the study.

CALL NOTES

Red-throated Ant-Tanagers.—The note most often used by Red-throats was an extremely rough, low-pitched call, commonly given at the rate of two or three per second in groups of two or three. Such notes resembled in quality the growls of an old car being started on a cold morning. Other ornithologists have referred to such noises as "wren-like" and "like tearing paper." I represented them as *waij jaij jaij,* or called them "scolds."

When Red-throats were greatly excited, as when they dashed away after I began to follow them, they occasionally gave staccato notes that resembled in quality the *scack-ack-ack*! of the Catbird (*Dumetella carolinensis*). The "chatter" of each Red-throat commonly included two to four notes, given at the rate of about six notes per second; at times several chatters were given in rapid succession. Males uttered such loud chatters more often than did females. Once a fledgling Red-throat gave a weak form of this chatter as a continuation of its *chut-chut-chip*! nest-leaving call.

The third common note of Red-throats was a low call barely audible at ten meters. I represented this note by *wik*.

Red-crowned Ant-Tanagers.—Although Red-crowns had a greater variety of notes than did Red-throats, they seemed to lack calls comparable to the scolds of the latter. Instead, the most frequent call of Red-crowns was a rapid series of as many as fifty (commonly five to fifteen) staccato notes, given at the rate of about six per second. At times the pitch and/or quality changed one or more times, as *chit chit cheut cheut cheut,* during a "chatter." Chatters were definitely modifications of *chut-chut-chip* calls, as young birds 15 to 20 days after hatching had calls intermediate between the two sound types. Males were less prone to chatter than were females.

A low-pitched *chook*, resembling the call of the Hermit Thrush (*Hylocichla guttata*), roughly corresponded to the *wik* of Red-throats.

There were many other faint notes that Red-crowns uttered: a soft, musical *ch'ree* (mainly from males); a low *ch'r*; a *wreed reed reed*; and so on. The many calls I recorded can be arranged in a number of intergrading series, and the more musical were hard to distinguish from songs.

A male observed eight kilometers northeast of San Blas, Nayarit, México, on December 28, 1959, had similar calls; but the chatters and *ch'ree* were rougher and more nasal.

SONGS AND SINGING BEHAVIOR

Each species of ant-tanager had two distinct major songs, which I shall call "day songs" and "dawn songs," although the implications of these names are correct only for Red-crowned Ant-Tanagers.

Red-crowned Ant-Tanager.—Rough chatters graded into the somewhat burry *cheer cheer cheer cheer* (fig. 1C) of the simplest day song merely by a slowing of the tempo from more than four to about two or three notes per second and, apparently, by an elision of some of the tones so that the rough noise became a fairly pure whistle. In all the variants of the *cheer* type of day song each slur or couplet descended in pitch; a type of day song in which each slur or couplet rose in pitch was nearly as common. The males seemed to say *pirtee pirtee pirtee pirtee* in the latter type of day song. Variants and combinations of the two song types were numerous.

Day songs varied in the number of notes (one to ten, but usually three or four), in force, and in frequency of delivery. As the singing male turned his head the volume of

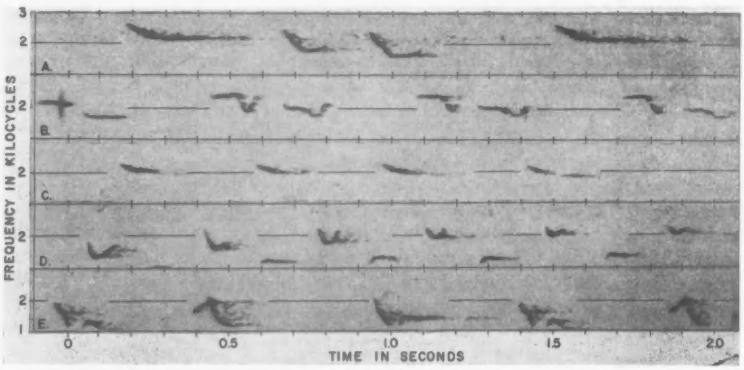

Fig. 1. Narrow-band audiospectrographs of ant-tanager songs. A, *peer, p'yerk pewk, peer,* dawn song of Red-crown from 10 miles south of San José del Carmen, Veracruz, México. B, *purtor, peter, peter, peter,* dawn song of Red-crown from Gallon Jug. C, the *cheer, cheer, cheer, cheer* day song of same male as in B. D, *purtor purter pur tirpee tirpee tirpee,* day song of a Red-throat from mountains above Tuxtla Gutiérrez, Chiapas, México. E, *ch'bewk, whewk, ch'berk, ch'bewk, whew,* fragment from dawn song about three times this length, from male Red-throat near Coatzocoalcos, Veracruz, México. (A, D, E by Irby Davis.)

the song waxed and waned, suggesting that the whistles were directional in nature. Figure 2 shows the variation in the frequency of one male's songs at a time of day when songs were most regular. When a male was singing uninterruptedly, some ten to twelve songs were uttered per minute; pauses between songs were as long to twice as long as each song.

Singing males often foraged, chased females, disputed along a territorial boundary, or occupied themselves with other activities. The males adopted no special postures; only the opening of a bill, a slight downbeat of the tail with each slur or couplet, and a pulsing of throat feathers as a male looked around showed the origin of a voice. Occasionally males sang in flight or when eating, but consuming large insects or fruit usually halted singing temporarily.

Day singing began in 1957 in late February, about a month before the females began building nests. For a time song was infrequent, but by the end of March all the adult males were singing, especially in the two or three hours after sunrise. Red-crowns were still singing when I left in early August, but the song periods were as short and infrequent as in early March.

In contrast to day songs, dawn songs varied detectably between individuals, and each individual rarely had more than one type. The simplest type of dawn song, a flutelike *peter peter peter*, was seemingly a strong and deliberate day song. Only 11 out of 24 males I heard at Gallon Jug had dawn songs audibly different (fig. 1B) from this type. Songs recorded by L. Irby Davis in Veracruz (fig. 1A) differ no more from songs I heard in British Honduras than some of the songs at Gallon Jug differed from each other.

The dawn song of the immature male of one family, first heard on May 24 in a whispered version, had by July become indistinguishable from the dawn song of the adult male of that family. The adult males on two adjacent territories had a similar song type, but the adult males on two other adjacent territories used the simple *peter peter peter peter* type.

The three-quarters of an hour before the sun broke through the low dawn clouds over the ridge east of the study area was the usual dawn-song period (fig. 3).

Unlike day singing, dawn singing was seldom interrupted by other activities. The first few songs, as each male moved from back in the forest toward his dawn-singing area, were often short and somewhat irregular in frequency of utterance. But as each male reached his song area, dawn songs came with clocklike regularity; he even sang in flight as he ascended from perch to perch toward his station.

Individuals differed in their singing rates, for some averaged only 8 songs per minute while others averaged up to 12. The full-length songs of the main period of song came about the same number of times per minute as the short versions of the beginning and end of the period. None of the birds at Gallon Jug gave more than six slurs or couplets per song; but on the Pacific slope near Colomba, Guatemala, Skutch (1954) heard Red-crowns giving seven to nine notes in their dawn songs. Males near Skutch's home at El General, Costa Rica, chanted monotonously, somewhat in the fashion of the dawn singing of Red-throats. No Red-throated Ant-Tanagers occur in that part of Costa Rica.

Most males on my study area (fig. 5A) sang from the edge of the forest, on a road or beside a plantation or patch of second growth. Males with territories which did not border on such areas sang in isolated treetops rising above the level of the surrounding forest. The dawn-singing station generally lay near the edge of each territory, not in the center. This might have been because the open areas were generally at the edges of the ant-tanager territories mapped here rather than within them. Whether there is any tendency for territories to radiate from open areas within the main forest is not known. Nor do I know whether the song areas tend to be on the peripheries of territories in less broken woods than those of the study area. Commonly two or three males sang near each other, even in areas of unbroken forest.

The favored perches were most often below the tops of song trees, on bare branches near the centers of the trees rather than in dense peripheral foliage. Hence the males sang from perches quite different from their usual foraging perches in the undergrowth.

Often males that sang close to the ground became nervous as I approached, turning back and forth and hopping about. If I moved closer, they flew to other perches. One such male moved from one perch to another around a small cornfield when I entered it, once singing from a log on the ground. The birds that sang 25 meters or more up rarely moved more than a meter while I watched.

The dawn-song period was the only time that the brilliant scarlet of the Red-crown crests was consistently displayed. Every bird I saw seemed capped by a crown of fire

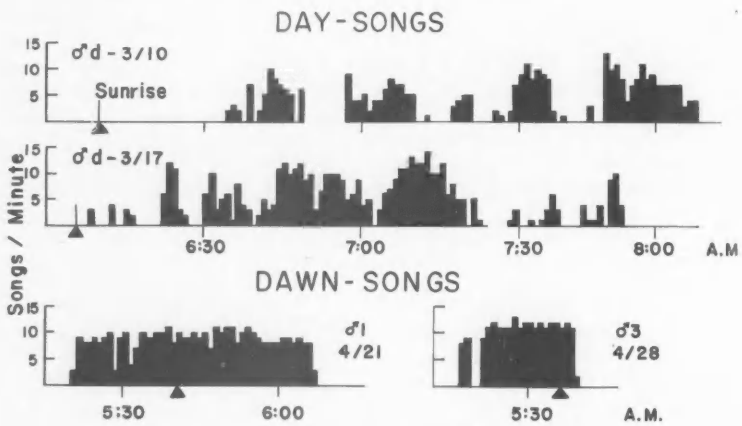

Fig. 2. Timing of day songs and dawn songs of Red-crowns.

during the whole period. Even later in the day, on the few occasions when one uttered dawn songs in boundary disputes, each repetition of the song brought a lifting of the crest, followed by a drop before the next song. Some adjoining dawn-singing males may have been able to see each other, but most males probably could not; however, the females wandering about nearby undoubtedly could see their fire-crowned mates at times.

During most of the dawn-song period a singer typically held his tail and body in line, little inclined above the horizontal. His body plumage was seldom fluffed out although his tail was often partly spread. His looking around was interrupted only for a song, which he usually gave with beak in line with the body, throat pulsating, beak moderately open, body quivering slightly, and the tail jerking a little at each slur or couplet. Less often the singer sat with tail down like a flycatcher or singing finch, or hopped along the limb as he sang.

As the sun broke through the morning clouds the chatters of the female and other members of the family came now and again from the nearest forest edge or below the male, and he began to move about more actively. Eventually he flexed both wings, looked around, and dropped shrike-fashion to about two meters above the ground before leveling off to streak away toward his family. At times the drop was made in steps, with a song or two at each stop; on a few occasions a last song or two drifted back from the interior of the forest after the male's descent, or irregular singing persisted there for several minutes. But more often a silent descent was followed within a minute by an

outbreak of chatters and *chauf chauf* notes as the male chased his mate about. Then the first day songs began, and the family went off to the affairs of the day.

When bringing food to young in the nest, engaging in territorial disputes, or shaking vigorously after bathing, the Red-crown males poured forth at times what Skutch (1954) has aptly described as a "softly warbled refrain of singular beauty." Often the singer quivered with his warbling, fluttering his wings rapidly and raising his tail in the manner of a female in the precopulatory display. Among the commonest sounds of the

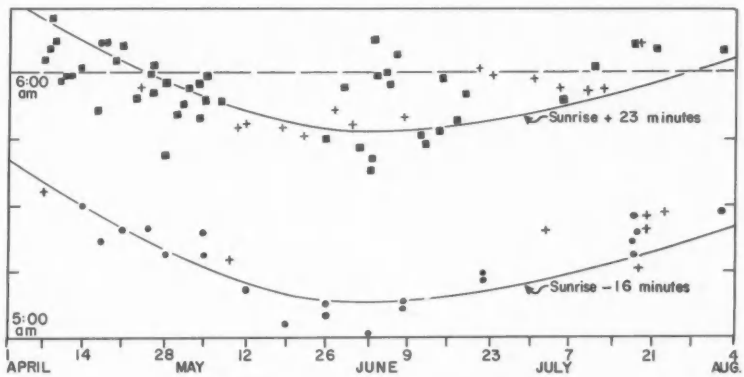

Fig. 3. Times of beginning (dots) and end (squares) of dawn songs of Red-crowns. Crosses indicate singing was in progress.

warbling were two that may be represented as *turee-e-e-e* and *kiss'l*. At territorial encounters, but rarely at other times, rough and low chatters and sometimes a day song or two were intermixed with the warbling.

Red-throated Ant-Tanager.—The day song of Red-throats was a rapid series of whistles that bore no resemblance to their harsh scolds. In its alternation of two kinds of notes on a rising scale (fig. 1D), this song was quite different from any song of Red-crowned Ant-Tanagers. The song may be represented as *pur'-tor-pur'-ter-pir'-tir-pee'-tir-pee'*.

The day songs of Red-throats averaged 11 to 15 notes in length. The speed varied considerably, averaging five notes per second. Amplitude ranged from soft to loud within a single song. At the nest, songs were barely audible at ten meters, although the loudest songs were audible through the undergrowth at over 100 meters. I could never detect differences between individual males, although from one song to the next a singer often varied his songs. At times a low squawk ended a song, or the first few notes of a song were repeated as a low-pitched ending.

There were often long intervals between day songs. About four songs per minute were usual during uninterrupted singing, and there were rarely more than seven per minute.

The peak of day singing came in the hours from 5:30 to 9:30 a.m. (fig. 4). I never heard the day song before civil twilight in the morning nor after sunset in the evening. Day singing was at its height during the nesting season, although for a month before nesting this song could be heard nearly every day. In the rainy season, as other forest

birds became quiet, Red-throat singing slacked off abruptly; and after July 21 day songs were rare, although Red-throats were still nesting.

While singing, Red-throat males looked around as if foraging, tails no more spread and bodies no more fluffed than usual. Although I never saw a male eat during a song, in the way that Red-crowns did, Red-throat singers occasionally interrupted singing and captured an insect or other arthropod.

The dawn songs of Red-throated Ant-Tanagers were deliberate chants, strikingly different from the dawn songs of Red-crowned Ant-Tanagers. In its simplest form at

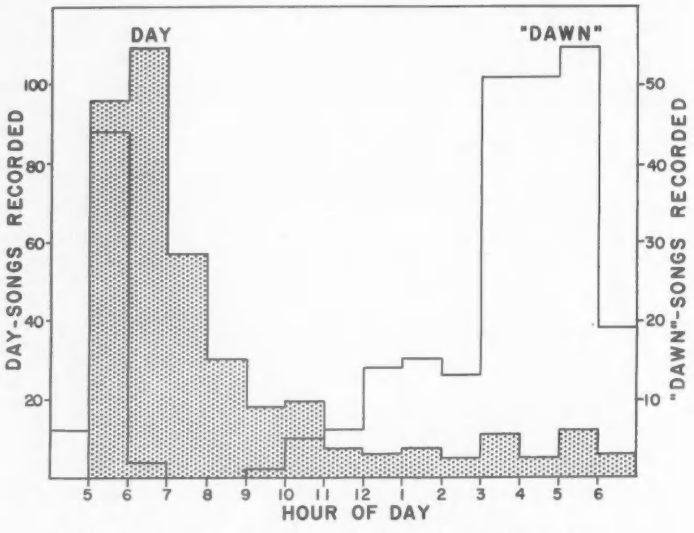

Fig. 4. Hourly record of day songs and "dawn" songs of Red-throats.

Gallon Jug the dawn song of the Red-throat was a measured chant of two or more (commonly 12 to 15) staccato notes in phrases of three: *chuk, per, chick, chuk, per, chick, chuk* and so on. Four out of 14 males on my study area used such a song. The most complex of the variants used by the other males were the closely similar songs of adjoining males XI and IX (fig. 5B); *pee-oh, perk, chork, p'ree, cherk-puk-peeoh, perk, chork, p'ree, pee-oh, perk* and so on. Figure 1E is an audiospectrograph of a song recorded by L. Irby Davis near Coatzocoalcos, Veracruz, México; it differs little to my ear from songs at Gallon Jug.

Dawn songs were given at a steady pace of about two notes per second. Exact repetition of phrases was not the rule; one or two notes in a phrase might be varied or omitted. The songs began and ended on any note of a phrase, giving the songs an incomplete sound when the ending did not correspond with the end of a phrase. Usually five or six songs were given per minute during uninterrupted singing, rarely as many as nine. Neighboring singers often had similar songs, as did Red-crown neighbors. An occasional male Red-throat used a dawn song similar to that of a neighbor when the neighbor was singing, whereas he used a different song at other times.

Dawn singing was mainly restricted to the actual nesting period, which started in

early April in Red-crowns and in late April in Red-throats. At times of noisy scolding at dawn and dusk, I heard a dawn song of a Red-throat once in February and once in March.

Unlike the dawn singing of Red-crowns, the dawn singing of Red-throats was not restricted to the hour of dawn: I have heard these songs at every time of day except the period from 5:45 to 9:15 a.m. (fig. 4). The two early records for Red-throat dawn singing are 4:43 a.m. on May 26, 18 minutes before civil twilight, and 4:56 a.m. on June 3, 5 minutes before civil twilight. The late record is for 6:50 p.m. on July 10, ten

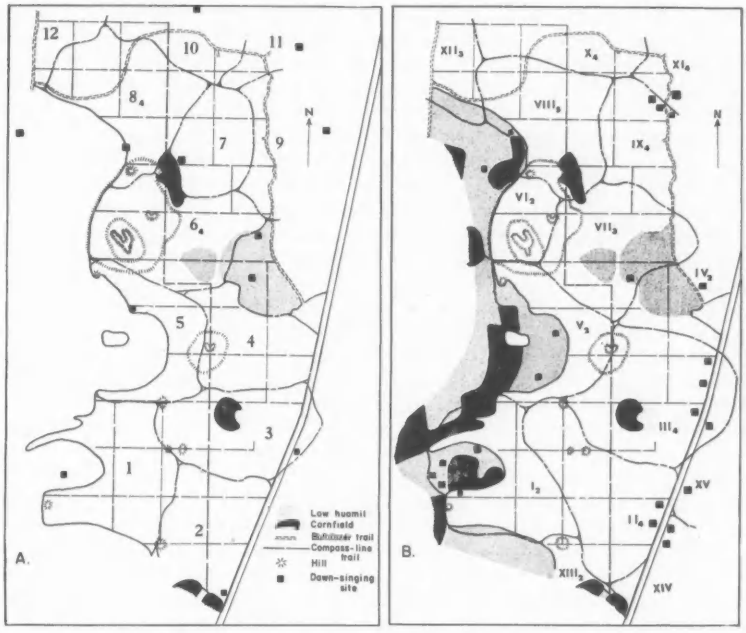

Fig. 5. Territories of pairs and families of ant-tanagers on study area at Gallon Jug. Length of arrow represents 100 meters. A subscript to a territory number indicates number of birds occupying that territory. A, Red-crowns; B, Red-throats.

minutes after sunset. The dawn songs of Red-throats came sporadically at times, broken by long pauses or short periods of day singing. But at other times two males sang in alternation, or both chanted nearly continuously.

The end of singing occasionally came long before nearby Red-crowns finished dawn singing, but at times it ended only a few minutes before the Red-crowns stopped. One Red-throat male consistently sang late, up to 15 minutes past sunrise, even after an adjacent male Red-throat started his day songs.

The dawn-singing areas of Red-throat males were less restricted than those of Red-crown males; male I (fig. 5B) was heard singing at one time or another over the whole western half of his territory. Commonly the areas used by Red-throat males were patches of thick second growth a year or two old or the dense edges of the forest along a road,

trail, or cornfield. While singing, the males moved now and then, often with a chatter in changing perches. I was unable to creep up on them through such thickets, but fortunately happened to see a singing male once while I was sitting in a blind: "July 9—5:07–5:10 p.m. male sings near Red-crown nest. His crest is compressed, not displayed, and he is not particularly fluffed out. He sits with tail down (not spread) in finchlike pose, the only movements those of his head. To chant he merely turns his bill forward, and bill and throat feathers move slightly. Finally he turns around, leans forward into a more tanagerlike pose, and flies off a few meters to resume singing."

It is perhaps noteworthy that his crest was definitely concealed under his crown feathers. Except for one time when a male was giving a chattering and scolding series near an ant swarm, I have seen male Red-throats display their crests only during preening; I wonder if their crests are functional. Certainly, in the three species of the genus *Habia* only the crests of Central American members of the *Habia gutturalis* complex are short and rather dull in males and undifferentiated from other parts of the crown in females. *Habia gutturalis gutturalis* of Colombia, in which both sexes have long and bright red crests set off vividly by dusky bodies, is possibly a different species from the Central American members of the complex, as Eisenmann (1955) has suggested. Males of *Habia rubica* have bright and fairly long crests with contrasting dusky borders, although their females have yellow crests that are much less striking than the red crests of females of *H. g. gutturalis*. *Habia cristata* of the Colombian Andes has a longer crest than *H. g. gutturalis*.

Since dawn-singing Red-throat males sang far apart in dense undergrowth, and since their dawn songs were generally given while females were on their nests, probably crest raising could serve no communicatory function in a dawn-singing situation. But Red-crown males, which consistently raised their crests during dawn singing, often sang from conspicuous perches while their mates were nearby.

COURTSHIP AND MATING

The *chauf* notes of Red-crowned Ant-Tanagers consisted of one to several very rough, low notes that in quality approached some scolds of the Red-throat. Male Red-crowns at times used such notes, especially when chased by another bird of the family in a food dispute. Frequently while the female of one Red-crown family was on the nest, the adult male chased the immature of the family. The immature gave *chauf* notes each time, but my supposition that it was a female was proven wrong when the young bird started acquiring red male feathers in July. However, the *chauf* notes were most often uttered by females being chased by their mates. These notes were among those frequently used when a female flew past her mate on leaving the nest; he chased her if he did not have food for the young. Although the immediate effect of such *chauf* notes was to break off a chase abruptly, the male often chased his mate again after a brief pause.

Female Red-throated Ant-Tanagers had, instead of special "chase" notes, outbursts that were generally associated with the day songs of their mates. Such outbursts consisted of light scolds interspersed with rapid conversational notes; I represented one such series as *waaj-tuk-tuk-waaj-tuk-tuk-tuk-waaj-waaj-waaj-waaj*. The effect can be approximated by whispering the word "agitate" very rapidly, with emphasis on the "ag" parts. The first time I heard day songs and such female outbursts was on March 23, when, in one of the first territorial disputes I witnessed, one female started these calls during day singing of the males and both males started chasing her. This was the only time when male Red-throats were seen to chase a female. Either the start of the female's outbursts set the male off on each day song or she detected when he was about to start, for her outburst rose in speed and volume a second or so before his song and continued

at a high level during it. The male usually sat calmly as he sang, but the female turned from side to side and dashed about rapidly. The *waaj-tuk* outbursts were among the notes used by females leaving the nests when their mates arrived with food for the young, a situation in which the males usually gave day songs.

The precopulatory displays of female ant-tanagers of the two species were similar in several respects. As a female of either species fluttered her spread wings through a small arc, she lifted her tail like a Hermit Thrush in slow motion. The latter action revealed her anal circlet as her abdominal feathers drooped nearly to the perch on which she stood. At times the female tilted far forward in her displaying and in returning to a more normal position went into an "upwards" position (a rather similar posture is illustrated for thrushes by Dilger, 1956) with bill up and throat prominent. At low intensities of display, when the precopulatory notes were uttered briefly, only slight quivering of the wing tips was retained from this behavior pattern. Even following copulation a female might repeat the performance over and over, with brief pauses when she looked around for food or preened busily. Displays were usually given at normal foraging heights. Once I saw a female Red-throat display on the ground in a bulldozer trail, but horizontal limbs and twigs were the usual places selected.

One difference between displaying female ant-tanagers of the two species was in the notes they gave. The notes of Red-crowns were *che* notes given so rapidly that the series sounded like *che-e-e-e-e-e-e-e* to me. The notes of female Red-throats were slower and more variable, a *chee cheu chee cheu cheu cheu* like the peeping of a flock of baby chicks, averaging some six notes per second. Another difference between female Red-crowns and female Red-throats was in the spread of their crests. The crest of each female Red-crown was ruffed up and showed its yellow center as at no other time, whereas female Red-throats, which lack such a decorative center, barely raised their crown feathers. It was my impression that female Red-throats looked around with bills pointing up more than did female Red-crowns; the bright yellow bibs of the former were made conspicuous by this movement. Although female Red-throats spread their fluttering wings up, out, or down, I never saw a female Red-crown spread her wings in any direction but slightly above horizontal.

Males of the two species differed little in their precopulatory behavior. Both hopped or fluttered toward their females with tails down and spread, the feathers perhaps fluffed a little. On some occasions male Red-crowns held their wings upstretched for the brief moments they were on the limbs beside their females, both before and after copulations. Once a male Red-crown uttered a loud series of *jee* notes when he flew to the female, and at times a few faint notes preceded the copulations of either species, but usually actual coitus was silent. The females were nearly always concealed from my view in fairly dense foliage when the males went to them. Copulations were sometimes followed by bathing or preening sessions. Rarely an immature bird came up near a displaying female, and one immature Red-throat crowded the female off her perch; but I never saw an immature attempt copulation.

The precopulatory calls of female Red-crowns were given at all stages of nesting except for periods when a female was searching for a nest site. But I noted high-intensity displays and actual copulation only during nest building and egg laying. Red-throat females limited their displays in the main to the two latter periods.

Although in voice and behavior of both sexes there are many interspecific differences that may reduce the possibility that mixed pairs of ant-tanagers could form, persist, and give rise to interspecific hybrids, the important process of pair formation is as yet unknown for these birds. All the males on my study area had mates when I arrived, and they probably stay mated all year. Unfortunately, I did not see how one male obtained

a new female when his mate was killed by a Ferruginous Owl (*Glaucidium brasilianum*) as she returned to her nest with food for her young at noon on May 26. The next noon this male had a new mate, which he chased with great vigor and persistence; a *chauf* series came from the female each time he chased her. The new female began a new nest the following morning.

DISPLAYS AND TERRITORIALITY

The two species of ant-tanagers held territories overlapping interspecifically but not intraspecifically (fig. 5), which implies that each species could somehow distinguish its own species from the other. The ability of the birds to recognize their own species by voice was obvious. The sound of distant song and chatters of Red-crowns brought eventual investigation by a male Red-crown whereas it would leave nearby Red-throats unmoved. When I whistled Red-crown day songs in the forest, only Red-crowns came up and investigated. A distant song or scold of a Red-throat never brought any response from a Red-crown pair, but it often brought forth a song or two from accompanying Red-throats, with perhaps rapid movement toward the intruders.

Some experiments were performed to test whether the two species can tell each other apart when one or both are quiet. Dilger (1956) tested five species of thrushes of the genus *Hylocichla* with painted models and found that all models were attacked indiscriminately unless he played back a recording of the voice of another species when he presented the models. To see if the ant-tanagers were unable to tell their own species from another by sight alone, I placed before them mounted specimens kindly prepared by P. A. Daigre. These were employed in about the same manner in which Dilger used his painted models before he played recordings. Since the mounted birds could not give vocal or behavioral cues, any recognition by the ant-tanagers would be based on appearance of the mounts alone.

On the five occasions when the mounted male Red-throat was set up within two to seven meters of different Red-throat nests, the resident male at each nest attacked it violently on his first return, although not on later visits. Five times when a mounted male Red-crown was set up in similar positions it was ignored; the models were left up for two to four hours on each occasion. On another occasion, when I set the male Red-crown up so that its left eye was oriented directly toward the Red-throat nest and about five meters from it, this reaction ensued: "May 27—(female, male, and immature just back to nest; female with material). Immature flies over my blind to the tree on the other side of the nest, scolding noisily, with tail spread. Female freezes on nest, and male comes up and looks at *Habia rubica* mount. He sits with tail spread and breast ruffed out. Then he hops around in front of mount and starts a very faint irregular growl, holding his bill open and tail spread. Female resumes work on nest, but her movements are slow and inconspicuous, and she sits very still for long periods. Finally male flies away with immature, one of two scolding; and soon female follows." On the preceding day the local male Red-crown had been greeted by a similar display when he came near this nest; his reaction had been to retire a few meters and resume foraging. On only one occasion was the Red-crown mount attacked violently by a male Red-throat; but the attack was not as violent as that on the Red-throat mount I had just removed from the spot.

Twice when I put up a male Red-crown mount near a Red-crown nest, the male attacked it violently on his first visit. Twice when I put up the male Red-throat for two to three hours near nests that were being visited every few minutes by the pairs, there was no reaction. On a third occasion I set the male Red-throat only two meters from the base of the sapling in which Red-crowns were building their nest, and I obtained this

reaction: "June 13 (second visit of pair after start of test)—7:38.15 to 7:38.40 a.m. Female flies to nest from east with nest material and works as male flies to limb near her and looks down toward Red-throat mount. Tail down and spread, body fluffed, he flutters down past the mount, tilting it slightly. He fluffs out again as he perches under it, but then looks up and seems to lose interest, compressing feathers and flying off nearby." The crests of ant-tanager specimens show more conspicuously than the crests of live birds; when viewed from above, this mount showed a crest nearly as conspicuous as that of a male Red-crown in partial dawn-singing display.

The male Red-crown that reacted to the Red-throat mount had not helped his female at her first nest, but when I set up the mounts at this nest I obtained interesting reactions, one being the only reaction I ever obtained from a male bird distant from his nest. "May 3 at 8:12 a.m. I set up the mounted male Red-throat. At 8:19 male Red-throat I suddenly appeared on the log beside the mount. He looked, puffed out his abdominal feathers until they covered his legs, and kept his tail down and slightly spread. He hopped along the log silently, once stretching his bill and head upward. Then he flew at the mount, alighting on top of it, his wings up and fluttering. The mount tilted forward, and the male flew to a nearby bush. He looked back toward the upside-down mount and ruffed his body feathers again; but his head and crest feathers were compressed, giving him a small-headed look. He flew to the limb above the mount and pecked down several times at a pin sticking from its right wing. He fluffed out again, and flew off to another perch. Back to the mount he flew, pecking it a few more times. Then he departed silently, about 8:22 a.m. His tail was never spread much, nor his head and neck feathers." When I put up the male Red-crown at the same spot later that day, the female Red-crown behaved as if it were her inattentive mate. During both periods when I set the mount up she flew past it on leaving with *chauf chauf* calls followed by chatters and gave a few soft notes each time she approached the mount and the nest; but during an intervening period when I removed the mount her visits were as quiet as usual.

Hence it seems likely that the ant-tanagers were able to detect the slight differences between the two ant-tanager species on sight, although more tests are needed to be certain. What morphological cues are important in such recognition, and whether this ability is characteristic of the two species in areas where the two do not occur together, are also interesting questions for further investigation.

Meetings of two families of the same species near the common edge of their breeding territories were occasional in February and March; the groups foraged together peacefully for varying lengths of time before the trespassing group returned to its own area. But as the day songs of the males began, this cameraderie waned, and by the beginning of nesting each group had only one adult male, who tolerated no adult male intruders of his species on his territory. Now the females and immatures might chatter or scold as they foraged together with little sign of animosity, but their males disputed busily as the two groups moved along the boundary line between the two territories.

Although I was able to view the wary Red-throats at boundary disputes on rather few occasions, my observations are consistent in indicating that boundary displays are reduced to a minimum in this species. Crest and head feathers were sleeked down, but body and tail feathers were spread to varying degrees, as opposing males hopped along and looked toward each other. Ritualized movements were few and irregular; the only distinct one was an "upward wigwag," with beak pointed upward stiffly as the displayer turned back and forth in a wigwag or sparring motion. At times one bird opened its beak slightly, but no sounds emerged. Suddenly one male would dart at the other, which would retreat a few meters; or there might be no attack. Usually the pair I had been following moved back into its territory on a new course after a few seconds of such display. At

times a few day songs were exchanged as the pairs separated. Once I saw a male come back past his female after a rapid chase of another male down a boundary line. The body plumage of the returning male was puffed out as he fluttered along like an Eastern Kingbird (*Tyrannus tyrannus*) and gave a stream of *scack-ack-ack* chatters. Such loud chatters often burst from a male as he left after a violent attack on a mounted male.

Territorial displays of Red-crowns were more complex than those of Red-throats, although they were highly irregular compared to the stereotyped patterns of display of many birds. In Red-crown territorial disputes, songs played a major part. At times two males sang back and forth for some time without coming into sight of each other. But if a rival persisted in singing while foraging along or across the boundary between territories, the resident male sat with tail down for a minute or two and then darted through the forest toward the intruder. As the two males approached and faced each other, they uttered a varied assortment of day songs, chatters, warblings, and other notes. The louder songs were more frequently used when the males were far apart, whereas softer songs prevailed at close range; but loud *p'ree p'ree p'ree* songs occasionally poured out as two males foraged scarcely two meters apart. Otherwise the varied vocabulary fell into no consistent patterns.

Frequently a male picked off an insect or a berry and sang between gulps as he ate it. Because the males made a great show of foraging, a casual observer of a boundary dispute might think that the two families were foraging along peacefully together were it not for the varied songs and occasional displays.

Movements of the males such as their frequent bill wiping and looking at their feet may have had display significance. Occasionally bouts of spasmodic preening interrupted the more protracted disputes. The two males seemed to avoid looking at each other, but even when one foraged within a meter of the other each stayed on his own side. Crest and head feathers were usually sleeked down, so that the dark edges of the crown formed a zigzag seam that completely concealed the scarlet crest; but the tail and body feathers tended to be somewhat spread.

The only distinct display besides the wing quivering during warbling was the upward wigwag display. Unusual postures, some with wings outstretched, were used by males in attacking mounts, but not in boundary disputes.

Supplanting and chasing was uncommon. On the few occasions when a trespassing male had wandered some distance inside the owner's territory before the latter arrived, the owner sat quietly for an instant with tail down and spread. With no other posturing, he darted suddenly at his singing rival, which dropped backward off the perch after gaping briefly. At times there were two or three such attacks before the intruder was near enough to the boundary that the usual singing and foraging began once more. A bird attacking a mounted bird pecked at it as he hit it and knocked it over.

One immature was an active participant in boundary disputes. The adult male of the family never displayed against his immature, which was developing dawn song and day song while I was there, and the immature came to help him in boundary disputes with adjacent males. As early as April 17, when the immature was singing infrequently, it helped the adult male in a dispute with another male; the latter directed a supplanting attack at the immature even though the adult male sat singing nearby. By July, when the immature male obtained his first red feathers, he was even more eager for battle than his adult male. The immature then engaged in warbling and display duels with rival males while the adult male sang day songs out of sight some 30 or 40 meters from the boundary. Why did the adult male not react to his immature's songs in the same way that other males did?

Territorial disputes were most frequent on boundaries in parts of the forest where

the undergrowth was sparse. As Red-crowns spent much of their time foraging in such areas, this might have been expected; but other boundary lines in similarly sparse undergrowth rarely were defended. Certain males argued frequently along certain boundaries and hardly ever disputed with other males on other boundaries of their territories.

Territorial disputes of Red-crowns were often prolonged. One dispute between three males lasted at least 65 minutes before the males separated. The average length for 52 disputes was about 17 minutes.

Six territories of Red-throats averaged about 5.7 hectares (15 acres) in extent while eight Red-crown territories averaged about 4.5 hectares (about 12 acres). When one male Red-crown disappeared, seven males occupied 5.2 hectares each. Territories were mapped by following families; generally points of boundary disputes counted as boundaries, while on segments where no disputes were seen the mapped lines (fig. 5) lie near the midpoints between the wanderings of each two pairs, whether these wanderings overlapped or not. Fortunately each pair ordinarily wandered over its whole territory looking for food, and it rarely trespassed more than a few meters into areas where I followed the neighboring families at some time during the nesting season. Dawn-singing areas of

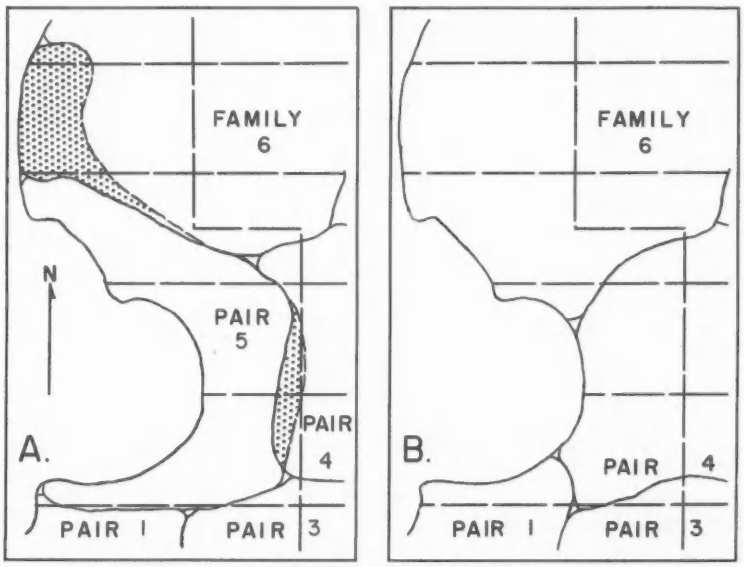

Fig. 6. Changes in the ownership of territory 5. A, February to April. The territory added by male 5B is stippled. B, May to August.

males are not included in their territories when the males sang from areas they never used at any other time.

The censuses of Davis and his co-workers in México (1952, 1953*a*, 1953*b*, 1953*c*, 1955, 1956) have generally reported denser populations of both species on sample plots of 15 acres (about 6 hectares). Most of their estimates show from two to four territorial males per sample block, which if literally interpreted would mean two to five times the density of breeding males I noted at Gallon Jug. However, the probability that most of

the males Davis and his companions recorded had only parts of their territories in these small sample blocks must be taken into account. Other than these censuses, I know of no other estimates of ant-tanager density.

The changes following the disappearance of Red-crown male 5 on April 8 after 7:08 a.m. were quite interesting (fig. 6). He was not at his dawn-singing post the next morning, and that afternoon as I followed pair 4 they drifted across into the territory of pair 5. Male 4 sang occasionally, but no challenges came from any resident male or female.

On April 10 at 3:18 p.m. a new male, distinguished from other males on my study area by two green feathers separated by a red one in his tail, was busy in a boundary dispute with male 6 near the top of the hill near the north end of pair 5's old territory. Whether the female with this new male was the original female 5 is unknown. In the following days disputes between male 5B and neighboring males 4 and 6 were frequent and vigorous, as 5B established his territory over and beyond the area that 5 had defended. By the end of April, 5B had taken up the same dead tree that 5 had used for a dawn-singing perch and was alternating a *peter peter peter peter* such as 5 had used with a variant of his own. But May 2 was the last time I heard his dawn song, and for a time there was no replacement.

Within two weeks, 4 and 6 had halved his area and were using the halves as parts of their territories. August 1, the day before I left Gallon Jug, I met a new, noisy pair in the south half of old territory 5. The male was just changing to the red adult plumage. Possibly this was an early stage of territory establishment.

SUMMARY

At Gallon Jug, British Honduras, the Red-crowned Ant-Tanager (*Habia rubica*) could easily be distinguished from the Red-throated Ant-Tanager (*H. gutturalis*) by its rapid chatter, quite different from the latter's rough and slow "scolds." Chatters were given at a rate of some six notes per second, scolds at a speed of about three notes per second. Other call notes of these sibling species also differed considerably.

The distinctive songs of male ant-tanagers included dawn songs and day songs. The dawn songs of Red-crowns and Red-throats were given at sunrise, but Red-throats also gave dawn songs in the afternoon; the "dawn" songs of the latter species were restricted in the main to times when their mates were not present. Male Red-crowns raised their scarlet crests prominently while engaged in dawn singing, but the seemingly nonfunctional crests of male Red-throats were rarely lifted.

Female ant-tanagers had species-specific "courtship" notes. The short, rough notes of female Red-crowns were used when males chased them; noisy outbursts came from female Red-throats when their males sang day songs. Chases were infrequent in the courtship of the latter species. The precopulatory displays of females of the two species differed mainly in the peeping notes that accompanied wing-fluttering and tail-lifting. The peeps of female Red-throats came at the rate of about six per second and varied in pitch; those of female Red-crowns came more rapidly and held a constant pitch.

Male ant-tanagers defended large territories during the breeding season. The males seemed able to tell a mounted male of the other species from one of their own species, attacking the latter and ignoring the former in most tests. The females and immatures of ant-tanager families rarely participated in territorial disputes between adult males, which usually came at the boundaries between territories. The displays of Red-throats at such boundary disputes were brief and uncomplicated bluff displays. Disputes of Red-crowns were prolonged exchanges of a great variety of songs and calls and a few displays, with intervals of foraging, preening, and other activities that may have functioned as displays.

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THE NEST AND EGGS OF THE SLATY VIREO

By J. STUART ROWLEY and ROBERT T. ORR

What is presently known as the Slaty Vireo (*Neochloe brevipennis*) was described by Sclater in 1857 from a specimen collected at Orizaba in Veracruz, México. In the next 87 years a total of six specimens, all from that state, were recorded. In 1944, Miller and Ray (Condor, 46:41–45) described *Neochloe brevipennis browni* on the basis of a single specimen taken near Chilpancingo, Guerrero. Since that time 23 more specimens, all belonging to the nominate race, have been recorded and the range of the species has been extended from Veracruz and Guerrero to Oaxaca. The published records are summarized by Moore and Medina (Condor, 58, 1956:442–444). It is interesting to note that only one of the thirty specimens recorded is known to have been a female. This specimen, secured at Amatepec, Oaxaca, is considered by Briggs (Condor, 55, 1953:157) to be of the race *brevipennis* and is indistinguishable, as far as plumage and measurements are concerned, from males taken at the same locality.

Fig. 1. Nest of the Slaty Vireo (*Neochloe brevipennis*).

On June 13, 1958, one of us (Rowley) had the good fortune to obtain a second female as well as what is believed to be the first nest and set of eggs of this species, in

the state of Morelos. The exact locality was in a pine-oak association three miles east of Cuernavaca, at an elevation of approximately 6000 feet, on the western slope of the Sierra Madre Occidental.

The nest, which was situated at about eye level on an oak limb, was discovered accidentally. During an intense storm a Slaty Vireo was seen moving nervously from branch to branch in an oak. On attempting to approach this bird another individual of this species flushed from a nest several feet from the observer. The second bird, a female, was secured as were the nest and eggs. The first vireo that was seen was presumed to be the mate of this female, but because of the heavy rain and strong wind prevailing at the time, it was not taken.

The nest is made entirely of plant material. The outside is covered with dried leaves and plant down, and the cup is lined with fine fibers. The external diameter is 75 mm. and the depth 65 mm. The cup measures 45 mm. in diameter and 45 mm. in depth.

The nest contained one egg of a Brown-headed Cowbird (*Molothrus ater*) in addition to three fresh vireo eggs. The latter, as is evident from the accompanying illustration, resemble those of most North American vireos in appearance. Their ground color is white and they are sparingly spotted, principally near the large end, with light and dark brown. They measure, in millimeters, as follows: 19.6 × 14.3, 18.8 × 14.1 and 18.8 × 14.0.

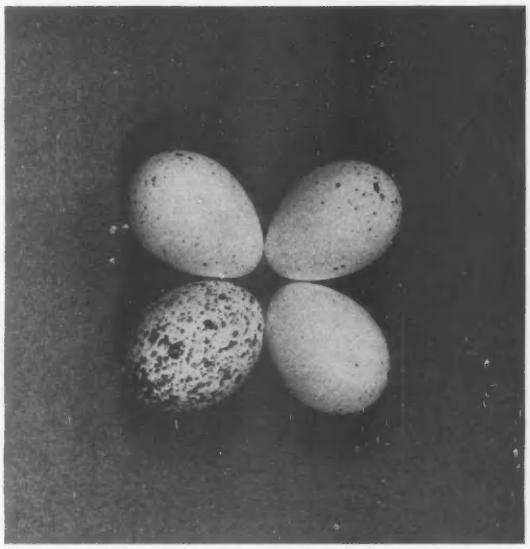

Fig. 2. Eggs of the Slaty Vireo (*Neochloe brevipennis*) and an egg (lower left) of the Brown-headed Cowbird (*Molothrus ater*) which was also present in the nest.

Although Cuernavaca is considerably north of Chilpancingo, the type locality of *Neochloe brevipennis browni*, it is west of the heretofore known range of *N. b. brevipennis*. In all respects, however, the female here recorded agrees with descriptions of the latter race, and it affords no evidence of sexual dimorphism in size or color of plumage. The back is gray and there is only the slightest tinge of green evident on the lower rump. The wing measures 56 mm.; the bill measures 6.6 mm. from the nostril to the tip and 3.4 in width at the anterior edge of the nostrils.

California Academy of Sciences, San Francisco, California, September 2, 1959.

CORRELATION OF VARIATION IN THE WRENTIT WITH ENVIRONMENTAL GRADIENTS

By DARL E. BOWERS

Correlations between environment and animal size or color have long aroused the interest of biologists and have stimulated the formulations of ecogeographical rules and the evaluation of the validity of these principles in many different animals. The questions that arose concerning the mechanisms governing correspondence between environment and the animal led to early, unsuccessful experiments to establish direct effects of humidity, temperature, and color of surroundings (Beebe, 1907; Ogle, 1934; Sumner, 1934; and many others) on captive animals raised under artificially controlled conditions. The geographical principle concerned with high levels of melanism found in vertebrates inhabiting humid regions, namely Gloger's rule, has been described in general terms many times. However, there is a paucity of evidence causally relating humidity and other environmental factors with color expression. It is even stated in a recent paper (Hamilton, 1958:336) that the adaptive significance of increase in pigment deposition with increases in environmental humidity is unknown.

The work of Sumner (1932) on *Peromyscus maniculatus* and *Peromyscus polionotus* indicates clearly that differences of pelage color in these mammals are under genetic control. Similar genetic analyses of wild species and races of birds have not been made in so far as I know, but there seems to be no reason to suppose that similar results would not be obtained in birds, and the genetic control of variation of a species such as the Wrentit (*Chamaea fasciata*) is therefore assumed.

The best evidence for adaptive value of presumably genetic factors of coloration is indirect in birds and comes from field investigations of the larks in which it has been found by Meinertzhagen (1951) and Bates (1936), especially for *Ammomanes deserti* of Asia, that the plumage coloration of various races of this species agree very closely with soil colors on which the races exist when the environments otherwise are similar. Thus dark birds are found on dark soils and light birds on light sandy soils. Behle (1942) has described the same close association between plumage colors and soil colors in the Horned Larks (*Eremophila alpestris*) of western North America. Both these birds are prey species for several predatory birds, and since they are open-ground dwellers, the need for concealing coloration, in this case correspondence with local soil color, is evident.

In the races of the Wrentit in northwestern California, there is variation of plumage color that presents a rather consistent clinal pattern. The darkest birds, ascribable to the race *Chamaea fasciata rufula*, exist in the coastal humid belt from San Francisco Bay northward. The lightest birds of the race *C. f. henshawi* occur from the southern tip of the Vaca Mountains in Solano County northward and northwestward. In between the two, the race *C. f. intermedia* is found (see Grinnell and Miller, 1944). This race has been thus named because the coloration of the breast and belly regions is somewhere between that of the other two. The aim of the present work is not to review the rather artificial racial entities but to consider precise correlations in a series of populations which grade sharply in color from the coast interiorward.

After collecting 267 specimens in fresh fall plumage, I noticed that there were also variations in several dimensions of the Wrentits. In addition to a study of the color variation, then, an analysis of some of the body parts was undertaken.

The geographic area of California under consideration, as shown in figure 1, consists of all of Marin, Sonoma, and Napa counties and the adjoining parts of Solano, Yolo, and Lake counties. Wrentits are inhabitants of chaparral and scrubby vegetation border-

ing forested areas. They are extremely sedentary, nonmigratory birds with an average breeding territory size, according to Erickson (1938), of about eight-tenths of an acre. The species ranges throughout the large growths of brush that cover much of the coast and inner coast ranges of the area of investigation. Densities vary and aggregations of Wrentits brought together at localized food sources may be found in the autumn. The sedentary mode of existence means that transmission of genetic characteristics between

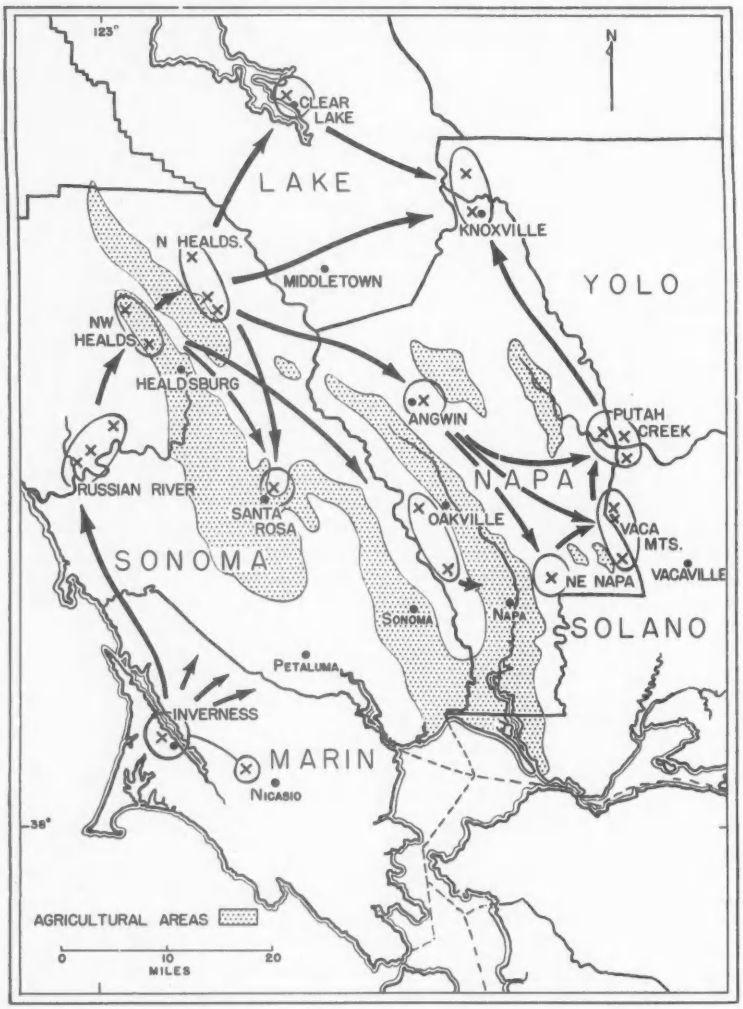

Fig. 1. Map of the area of investigation showing collecting localities (encircled) and color trends. Arrows point toward lighter colors.

populations is relatively slow, thus favoring establishment of clines. The lack of good habitat for the Wrentits in parts of the area studied has produced partial isolation of some populations.

I would like to acknowledge the assistance with plant identifications given by Dr. Helen Sharsmith and her associates in the University of California Herbarium under the direction of Dr. Herbert L. Mason. Dr. Mason also offered constructive criticism of the original manuscript. Dr. Frank A. Pitelka has kindly given assistance and valuable criticism concerning concepts and presentation of data. Dr. Robert T. Orr of the California Academy of Sciences generously made available to me the specimens in the collection there. Thanks are here expressed to my fellow graduate students who aided in the collection and preservation of specimens. To Dr. Alden H. Miller I owe a debt of thanks for his aid in the procurement of equipment and resources and for his critical assistance in evaluation of evidence and for guidance throughout the study and during the preparation of this manuscript.

ANALYSIS OF VARIATION

The specimens used for mensural characters were those collected by me in the autumn of 1951, 1952, and 1953, plus those skins in the California Academy of Sciences in San Francisco and those in the Museum of Vertebrate Zoology at the University of California, a total of 425. Color determinations and comparisons were made only from the 267 skins recently taken by me and obtained at the time of year when plumage is least worn, that is, when the feathers have just been renewed in the autumn after postjuvenal and postbreeding molts.

SEXUAL VARIATION

The females average smaller than the males in the four body dimensions of wing, tail, tarsus, and bill; they are also lighter in weight. The degree of difference between the arithmetic means for males and females varies from sample to sample. The back and breast coloration of new fall-taken specimens shows no significant difference between the sexes either in birds of the year or in adults. The color data for the sexes therefore have been combined.

SEASONAL VARIATION

Since there is but one molt period in the course of the year, once wing or tail feathers are free of basal sheaths, barring tip breakage, they are considered to represent their full lengths. As expected, birds collected in the spring and summer showed a higher incidence of broken feather tips than birds taken in the fall. Rectrices and remiges that had obviously been broken were not measured, but unobservable wear may have reduced some of the feather lengths. To analyze this influence, the data for the males of a relatively large sample of 73 birds from Marin County was broken down into two six-month periods for comparison. Measurements of birds taken from September through February were grouped, and those from March through August were handled similarly. September birds have largely completed their molt and hence have the newest plumage. The spring months are represented by birds carrying out breeding activities and these presumably would have the most shortened feathers due to wear. Such treatment shows that at least for this group of birds from Marin County there is no significant variation from one half of the year to the other.

Tarsal length is assumed to be constant the year around and throughout the life of the bird from the time it reaches its full size in the summer and fall of its first year.

Bill length is perhaps a more complexly variable attribute than tarsal length or feather length since the horny bill is growing continuously and is worn back at its tip by use. It is conceivable that the consumption of a seasonally changing diet or that addi-

tional feeding activity in the spring may produce differential wear on this part (see Davis, 1954). However, measurements of birds that were collected the year around are similar and therefore all have been consolidated for each locality.

Weight records were not adequate to make an analysis of the seasonal weight cycle.

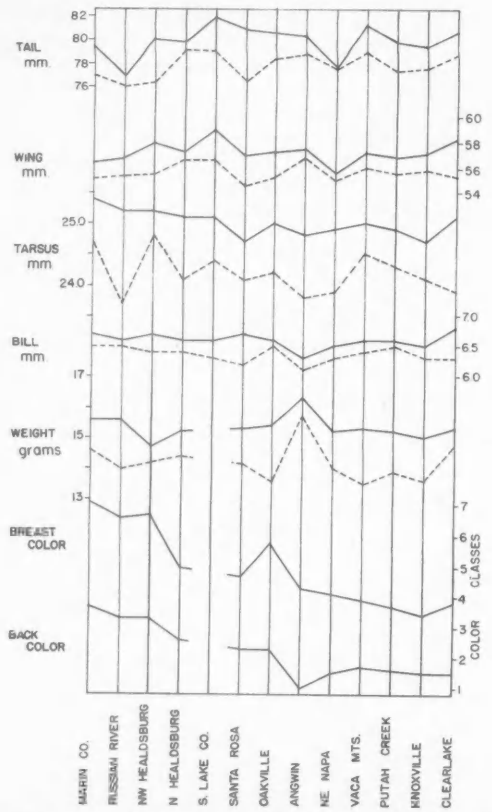

Fig. 2. Summary of mean values for all measurements and color determinations. Breast and back color classes are given some of same numbers but values for the two areas (see text) are not the same. For body dimensions, solid lines indicate males, broken lines, females.

AGE VARIATION

Comparison of the measurements of fall-taken, first-year birds (determined as such by skull examination) with those of adult birds has shown variable differences in dimensional characters. Some samples contain first-year birds that are larger than adults; in others they are smaller. In view of the lack of any consistent deviation of these immatures from the adults, plus the fact that the ages of most of the specimens from museums are not known, it has been judged that first-year and adult age classes may be combined. With regard to color, there is some indication that immatures in most populations

average slightly darker than adults. Statistically, however, there is no significance in this difference and for color comparisons the data from all age classes also have been combined.

GEOGRAPHIC VARIATION

Originally, the only significant geographic variation expected was in plumage coloration. However, analysis of measurable characters has shown some definite trends of statistical significance within the limited geographic range studied. The data for the various aspects analyzed are presented in table and graph form in which the localities are arranged in geographic sequences related to the color gradients to be discussed later. These mensural characters are all summarized in figure 2.

Wing length.—The chord of the right wing was measured. The main trends to be

Table 1

Wing Length (mm.)

Locality	Sex	Number	Range	Mean and standard error	Standard deviation	Coefficient of variability
Marin County	♂	71	53.0–60.4	56.50±0.19	1.57	2.8
	♀	60	51.3–58.6	55.07±0.21	1.59	2.9
Russian River	♂	19	54.4–60.5	56.96±0.37	1.58	2.8
	♀	9	52.2–58.5	55.37		
NW Healdsburg	♂	8	57.1–60.1	57.95		
	♀	4	53.2–57.4	55.45		
N Healdsburg	♂	11	55.5–60.0	57.33±0.39	1.24	2.2
	♀	9	54.1–59.5	56.73		
S Lake County	♂	21	56.7–60.6	59.00±0.27	1.19	2.0
	♀	14	54.8–58.6	56.69±0.33	1.20	2.1
Santa Rosa	♂	7	53.7–58.4	57.04		
	♀	6	52.9–56.1	54.48		
Oakville	♂	8	56.1–59.6	57.38		
	♀	5	54.7–55.9	55.34		
Angwin	♂	5	55.8–59.4	57.50		
	♀	4	54.3–58.7	56.83		
NE Napa	♂	8	53.1–57.7	55.62		
	♀	8	53.3–56.7	54.95		
Vaca Mountains	♂	31	54.1–61.3	57.83±0.28	1.55	2.7
	♀	22	53.1–60.6	56.15±0.39	1.78	3.2
Putah Creek	♂	27	54.5–60.3	57.41±0.30	1.52	2.7
	♀	30	53.2–58.8	55.64±0.26	1.42	2.6
Knoxville	♂	18	54.4–61.1	57.66±0.45	1.86	3.2
	♀	14	53.9–58.1	55.91±0.32	1.16	2.1
Clearlake	♂	4	57.2–59.3	58.28		
	♀	2	54.4–56.1	55.25		

seen by scrutiny of table 1 and figures 1 and 2 are toward longer-wingedness northward from Marin County and northward and northwestward from the Napa region. The birds from southern Lake County are significantly longer-winged than all others to the south. Statistical significance between samples in this study is based on the amount of overlapping, or lack of it, of the dimensions encompassed by the means plus or minus twice the standard errors of these means.

Tail length.—This was measured from the skin between the two middle rectrices to the feather tips (see table 2 and figure 2). In general, most of the trends are the same as those for wing length. The males from southern Lake County are significantly longer-tailed than those of all the samples to the south.

Tarsal length.—This was measured from the posterior aspect of the proximal end of the right tarsometatarsus to the distal edge of the last undivided scute. The only sig-

Table 2

Tail Length (mm.)

Locality	Sex	Number	Range	Mean and standard error	Standard deviation	Coefficient of variability
Marin County	♂	68	71.5–89.2	79.54±0.49	4.03	5.1
	♀	57	70.7–86.0	77.03±0.46	3.49	4.5
Russian River	♂	16	71.0–83.5	76.87±0.98	3.77	4.9
	♀	8	68.7–84.6	76.00		
NW Healdsburg	♂	8	75.4–85.2	80.05		
	♀	4	71.1–82.5	76.35		
N Healdsburg	♂	11	74.1–84.0	79.81±0.88	2.78	3.5
	♀	9	70.5–83.0	79.16		
S Lake County	♂	21	75.7–87.8	81.90±0.73	3.24	4.0
	♀	14	73.9–82.7	79.08±0.84	3.04	3.8
Santa Rosa	♂	7	76.8–88.3	80.87		
	♀	6	74.6–78.2	76.42		
Oakville	♂	8	78.0–85.5	80.69		
	♀	5	75.1–80.7	78.48		
Angwin	♂	5	76.2–83.8	80.26		
	♀	4	77.7–81.1	78.90		
NE Napa	♂	8	74.7–82.3	77.69		
	♀	8	74.2–80.2	77.54		
Vaca Mountains	♂	30	73.5–88.7	81.21±0.58	3.20	3.9
	♀	20	74.0–83.2	79.02±0.63	2.73	3.5
Putah Creek	♂	26	74.5–84.4	79.77±0.58	2.91	3.6
	♀	28	72.2–83.9	77.39±0.59	3.11	4.0
Knoxville	♂	17	73.4–85.1	79.36±0.93	3.75	4.7
	♀	13	72.6–84.1	77.61±1.08	3.73	4.8
Clearlake	♂	4	78.0–84.8	80.70		
	♀	2	76.4–81.2	78.80		

nificant difference with respect to this character occurs between the males of the Knoxville-Putah Creek region and those of Marin County in which the birds from the east at Knoxville have shorter tarsi than those of Marin in the west. In between, to the west and south of Knoxville, there is an irregular cline (see table 3 and figure 2). Tarsal length trends in the males seem to correspond most closely to those for color in which the shortest tarsi generally are found in the lightest birds and the longest tarsi in the darkest.

Bill length.—The measurement was taken from the anterior rim of the right nostril to the tip of the culmen. There are no significant differences to be seen here (fig. 2).

Weight.—Average weights lie between 14.7 and 15.6 grams for fall-taken male specimens and between 13.5 and 14.7 grams for female specimens (see table 4 and figure 2). No significant differences appear among the samples, which are admittedly small for seven of twelve localities.

Lengths in relation to weights.—Perhaps of more importance than linear measurements are ratios of these mensural characters to body size expressed as weight. These relationships have been examined in those samples of males in which weights for nine or more specimens are available. Average values for the four mensural characters have each been divided by the respective average weight values to give the mean number of millimeters per gram of body weight. These figures and those for weights are presented in table 5 for five localities studied intensively and are listed in a geographic sequence related to both the coloration gradient and to the average annual temperature gradient. To give a broader scope to this particular aspect, specimens in the Museum of Verte-

Table 3

Tarsal Length (mm.)

Locality	Sex	Number	Range	Mean and standard error	Standard deviation	Coefficient of variability
Marin County	♂	70	23.3–26.9	25.43±0.09	0.74	2.9
	♀	56	23.2–27.0	24.70±0.10	0.76	3.1
Russian River	♂	18	24.4–25.6	25.17±0.11	0.44	1.8
	♀	8	23.0–24.8	23.59		
NW Healdsburg	♂	8	24.6–25.8	25.24		
	♀	4	24.3–25.2	24.78		
N Healdsburg	♂	9	24.2–25.6	25.01		
	♀	8	23.2–25.1	24.09		
S Lake County	♂	21	23.9–25.8	25.03±0.13	0.59	2.4
	♀	12	23.2–25.5	24.37±0.23	0.76	3.1
Santa Rosa	♂	6	23.6–25.5	24.73		
	♀	6	23.0–24.7	24.05		
Oakville	♂	8	24.5–26.0	25.03		
	♀	5	23.6–25.1	24.22		
Angwin	♂	5	24.2–25.2	24.82		
	♀	4	23.6–24.0	23.83		
NE Napa	♂	7	24.3–25.4	24.94		
	♀	8	23.1–25.1	23.93		
Vaca Mountains	♂	31	22.4–26.4	24.99±0.14	0.78	3.1
	♀	21	23.5–25.8	24.50±0.15	0.67	2.7
Putah Creek	♂	25	23.4–25.9	24.86±0.14	0.70	2.8
	♀	29	23.2–25.4	24.35±0.10	0.53	2.2
Knoxville	♂	18	22.9–25.6	24.71±0.18	0.77	3.0
	♀	13	22.5–25.5	24.13±0.24	0.84	3.5
Clearlake	♂	4	24.8–26.0	25.10		
	♀	2	23.7–24.0	23.85		

brate Zoology representing the northern and southern extremities of the range of the Wrentit were analyzed in the same way to show the ratios for these same characters. These birds represent the races *C. f. phaea* from Oregon (9 males with weights); *C. f. rufula,* from Del Norte and Humboldt counties in northwestern California (14 males with weights); and *C. f. canicauda* from Baja California (37 males with weights). These data are also presented in table 5.

With reference to body weight, which gives an indication of size, it is apparent that shorter wings, tails, tarsi, and bills are present in the north and that there is a fairly even cline southward within the main study area that somewhat parallels certain climatic factors to be discussed later.

The longest wings, tails, and tarsi appear at the southernmost limits of the range of this species. The bills are longer there than in most of the samples from farther north. According to Allen's rule, extremities are relatively shorter in colder regions. This seems to be borne out by these birds, especially over the latitudinal extent of their range which likewise shows a temperature gradient of colder to warmer from north to south. Even within the restricted latitudes of the five study areas used here, there is some increasing length of extremities which correlates with increasing average temperatures.

Calculations of the Spearman rank-difference correlation were carried out. This statistic, rho, shows a correspondence between the rank-ordering of the eight localities with respect to the mean annual temperatures, as arranged in table 5 from cold to warm, and the rank-ordering of birds at these localities with respect to the mean number of millimeters per gram of body weight of the four measurable characters from short to long. The value of rho for wing length and temperature gradient is .926; for tail length,

.972; for tarsal length, .891; and for bill length, .788. The first three are significant at the .01 level and the last at the .05 level. This may be interpreted as a highly significant correlation between these measurements and the mean temperatures to be found at these localities.

Bergmann's rule, which states that animal bodies are relatively larger in colder

Table 4

Weight (grams)

Locality	Sex	Number	Range	Mean and standard error	Standard deviation	Coefficient of variability
Marin County	♂	25	14.3–17.3	15.60±0.19	0.91	5.8
	♀	22	12.9–16.4	14.57±0.19	0.85	5.8
Russian River	♂	6	14.6–16.8	15.57		
	♀	3	13.8–14.2	14.00		
NW Healdsburg	♂	8	13.0–15.6	14.68		
	♀	4	13.7–14.8	14.18		
N Healdsburg	♂	11	14.3–16.1	15.25±0.19	0.61	4.0
	♀	9	13.6–16.3	14.43		
S Lake County	♂	0				
	♀	0				
Santa Rosa	♂	6	14.8–15.9	15.33		
	♀	4	14.1–14.3	14.23		
Oakville	♂	8	13.2–17.5	15.46		
	♀	5	13.3–14.2	13.64		
Angwin	♂	2	14.7–17.8	16.25		
	♀	3	13.9–17.9	15.70		
NE Napa	♂	8	13.3–15.8	15.24		
	♀	8	13.2–15.2	13.99		
Vaca Mountains	♂	24	13.5–16.4	15.33±0.16	0.76	5.0
	♀	16	11.6–15.1	13.52±0.24	0.88	6.5
Putah Creek	♂	26	13.8–16.4	15.20±0.13	0.67	4.4
	♀	30	12.7–15.2	13.92±0.12	0.66	4.7
Knoxville	♂	11	13.0–16.8	14.95±0.35	1.09	7.3
	♀	7	12.7–14.5	13.57		
Clearlake	♂	4	14.2–16.2	15.33		
	♀	2	14.5–14.8	14.65		

Table 5

Measurements in Relation to Weight in Male Wrentits

	Average millimeters per gram				Weight in grams	
	Wing	Tail	Tarsus	Bill	Average	Number
Oregon	3.64	4.86	1.59	.428	15.76	9
NW California	3.51	4.62	1.57	.428	15.66	14
Marin County	3.62	5.10	1.63	.431	15.60	25
N Healdsburg	3.76	5.23	1.64	.435	15.25	11
Vaca Mountains	3.77	5.30	1.63	.431	15.33	24
Putah Creek	3.78	5.25	1.64	.436	15.20	26
Knoxville	3.86	5.31	1.65	.437	14.95	11
Baja California	3.94	5.42	1.68	.435	15.02	37

regions, also appears to apply here since the heaviest Wrentits are found in the north and lighter birds exist toward the south. Within the study area, the heaviest birds were encountered in Marin County where average temperatures are lower than at Knoxville where the lightest birds were found.

The rank-difference correlation between the rank-ordering of the eight localities with respect to mean annual temperatures from cold to warm and the rank-ordering of mean body weight for the birds at these localities from high to low has a value for rho of .937 which is significant at the .01 level.

Interdimensional correlations.—Correlations of habitat factors with these body parts may indicate some significant relationship. The chaparral studied and to be mentioned later shows varying densities. The most dense brush of these localities measured is found at Inverness in Marin County, the least dense at Knoxville. If birds living in

Table 6

Coefficients of Correlation (r) in Males

	Wing-tail	Wing-tarsus
Marin County	+.736	+.046
Russian River	+.502	+.367
N Healdsburg	+.547	+.387
S Lake County	+.596	−.228
Vaca Mountains	+.725	−.190
Putah Creek	+.802	+.085
Knoxville	+.749	+.269

the least dense brush tend to fly more, then perhaps longer wings and tails in proportion to weight (as found at Knoxville) may be advantageous and may thus be favored selectively. Likewise, less need to fly in the densest brush may lead to the selection of shorter wings and tails (as found in Marin County). Whether such correlations exist for Wrentits from Oregon and Baja California has not been determined.

Tail and wing lengths show reasonably parallel variations as is indicated by the values of the coefficients of correlation (r) shown in table 6. Presumably these appendages are related in their proportions first because they are made of the same material and very likely respond to the same growth controlling factors in the bird's body, and secondly because they constitute parts of the flight machinery which tend to have basic functional interrelationships of size.

If in dense brush the birds fly less and depend on hopping more than in less dense brush, then wing and tarsal lengths might be inversely correlated. For males they are correlated slightly positively in five samples and very slightly negatively in two samples as shown in table 6. On the other hand, it could also be argued that short tarsi are of advantage to Wrentits in dense brush and the positive values for r that are greater than the negative ones might be called upon to support such an interpretation. The low values of r, however, indicate no significant correlation either way.

Breast color.—Nine Wrentits, selected from the specimens in new plumage collected by the author, were used as color class standards by which to divide the total collection of 267 birds. These nine specimens represent the gamut of color expression within the limited geographic range under consideration and were carefully described by visual comparisons with color dictionaries and a disc colorimeter as well as by means of a photoelectric spectrophotometer to make sure they represented a reasonably objective color gradient. In adjectival color terms, inadequate as they are, the colors run from pale or light yellowish brown to moderate brown. These methods of color analysis have been discussed elsewhere by me (Bowers, 1956). The definition of the colors of all the specimens could in time have been carried out by using the procedures described there. However, it was considered that an adequate expression of the colors could be obtained by simply comparing all the specimens directly with these nine standard birds once

they had been selected. The testing of a second set of seven skins in the spectrophotometer gave evidence that fairly good equivalence could be achieved by the method of direct comparison since this second set was chosen by visual determination with reference to the first set.

The nine standard specimens were spread on a table before a large north-facing window in cloud-free daylight. The remainder of the skins, with the locality labels hidden, were then compared one by one with the breast areas of the standards and placed in a row headed by the one which was judged to be the closest match. In this way all the specimens were spread out on the table in nine rows. Some decisions were difficult because there are three dimensions in color and not just one as this kind of separation implies. The main aspect of color on which the decisions of position rested was that of value (darkness and lightness). Some birds that were obviously more yellowish or reddish than the standard that was closest in value were thus possibly placed out of proper position with respect to hue. Since of the three aspects of color the judgment of value is probably the most easily accomplished, it is considered that no great violence was done to the sequence of colors by this selection.

With the whole collection spread out, slightly different viewing positions were taken and a few birds that were seemingly misplaced were rejudged with respect to the other decisions made for that row. Some reassessments were made and better matches were thus found for those specimens in question.

The whole procedure was repeated on another day with the same physical conditions prevailing. For this second trial, 51.5 per cent of the specimens were the same as in the first trial and 95.3 per cent were judged as before or within plus or minus one step. The effects of these differences were shown in the averages of most of the locality samples although the greatest shift was only six-tenths of a color step. None of the color gradients between localities was reversed. These small shifts are thought to be not important since the overall picture still stands. The reproducibility is thus considered to be good especially in view of the problems of color dimensions mentioned earlier and also since there are relatively small steps between adjacent color groups.

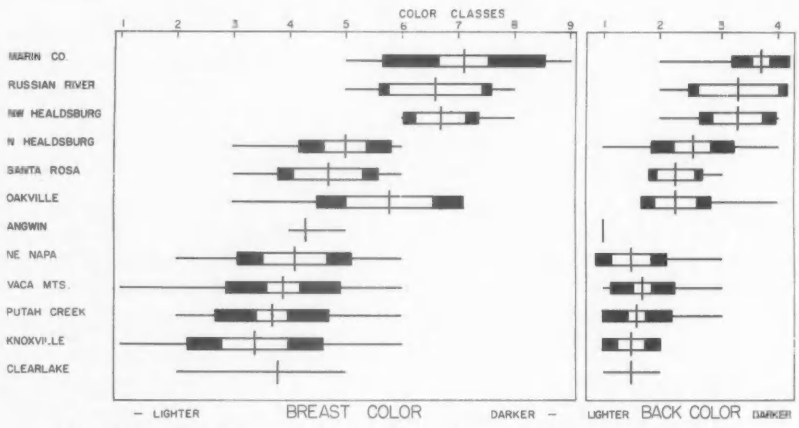

Fig. 3. Bar graphs for breast and back coloration. Ranges are shown by horizontal lines, means by vertical lines, twice the standard errors of the means by open bars, and standard deviations by solid bars.

For the present section the simple terms "darker" or "lighter" will be used to designate collectively the three dimensions of color.

By inspection of table 7 and figure 3, it is to be observed that there is a considerable degree of color separation between some of the samples. By comparing the graph with the map in figure 1, the geographic directions of these clines can be seen. The darkest birds are found in Marin County, the lightest in the Knoxville region to the northeast of Marin County.

Table 7

Breast Coloration

(Light to dark scale—1 to 9)

Locality	Number	Range	Mean and standard error	Standard deviation	Coefficient of variability
Marin County	44	5–9	7.11±0.22	1.44	20.3
Russian River	9	5–8	6.56±0.33	1.00	15.2
NW Healdsburg	12	6–8	6.67±0.20	0.67	10.0
N Healdsburg	22	3–6	5.00±0.18	0.82	16.4
Santa Rosa	11	3–6	4.73±0.27	0.89	18.9
Oakville	14	3–7	5.79±0.36	1.30	22.4
Angwin	4	4–5	4.30		
NE Napa	16	2–6	4.13±0.27	1.03	25.1
Vaca Mountains	54	1–6	3.87±0.15	1.08	27.7
Putah Creek	58	2–6	3.67±0.14	1.07	28.9
Knoxville	19	1–6	3.37±0.28	1.20	35.6
Clearlake	4	2–5	3.75		

The Wrentits from the Russian River, while only nine in number, average half a color step lighter than those from the Marin area but show much overlap with them. The twelve birds from northwest of Healdsburg, farther north, average approximately the same as those from the Russian River. There is good Wrentit habitat between these two collecting stations so that gene flow is probably relatively free between them.

The conspicuous break between those birds from the northwest of Healdsburg and those from directly north to slightly northeast of Healdsburg is striking. There is overlap between the breast color of the two samples only at the extremes of the range of variation of each and yet these collecting localities are fairly close together. There are two agricultural strips between these localities, and the specimens from northwest of Healdsburg were taken within one of these strips. The birds were found in field-side tangles of wild blackberry, poison oak, and *Baccharis*. Dry Creek, which runs northwest from Healdsburg, is flanked by riparian vegetation in which Wrentits were found. The agricultural areas which exist between these two collecting regions, although they contain some scattered Wrentit habitat, evidently contribute to a steepening of the color gradient.

If we consider the back color of these same birds, as shown in table 8 and figure 3, it will be seen that there is no overlap of twice the standard errors for these samples from northwest and north of Healdsburg. Thus in back coloration also there is a significant difference between these samples and the color trend is here steepened and runs in the same direction as that for breast color. The specimens from Marin County, Russian River, and northwest of Healdsburg then appear to form a cluster at the dark end of the color gradient and are set off from the rest of the specimens by the conspicuous discontinuity of the color gradient between the two localities near Healdsburg.

The Wrentits taken near Santa Rosa average lighter in breast color than those from north of Healdsburg, but not significantly so. The birds from the Oakville region average darker than those from Santa Rosa or north of Healdsburg, although they are lighter than those from northwest of Healdsburg. The meaning of these differences is not immediately clear. There is, however, a significant break between the breast color and also the back color of the specimens from northwest of Healdsburg and those from Santa Rosa.

Arrows may be plotted, as in figure 1, from Marin County through Russian River and northwest of Healdsburg, thence southeastward down to Santa Rosa and Oakville to indicate lightening colors. Arrows indicating such color directions would have to be drawn, considering averages only, from Oakville northwestward to Santa Rosa and also to the north of Healdsburg. This would cause confusing directions to appear along the Napa–Sonoma County line. However, since these reversals are not supported by signicant differences, they are only mentioned here and not indicated on the map.

There is almost a full step difference between the averages for north of Healdsburg and northeast of Napa. There is likewise only a slight overlap of twice the standard errors. Of course the distance between these two localities is roughly 40 miles and it could be expected that local conditions are different. Four specimens taken in February from near Angwin in Napa County, about halfway between Healdsburg and Napa, show intermediate coloration. Although these specimens are considered to be too worn for accurate color appraisal, they do indicate that the clinal direction on the map between these localities is correct.

It is of interest to note here that birds from Marin County are three color steps on the average darker than those from northeast of Napa. This difference is statistically highly significant.

The birds of Marin and those from Oakville, while on the average only a little over one color step apart, do show a significant difference. The habitat lying between these two localities is not suitable for Wrentits. There are large stretches of dry grassland and cleared agricultural areas that offer little good cover for the birds. This means that movement of Wrentits across the Petaluma–Sonoma–Santa Rosa region is probably quite restricted. Whatever continuity there is between these populations is maintained over more devious routes. Northward along the coast of Marin and Sonoma counties there is at least low scrubby coastal sagebrush in which the birds are resident. The connecting habitat is then interiorward bordering the Russian River and southward from Healdsburg along the mountains of the Napa–Sonoma County line.

Between Oakville and northeast of Napa there is the agricultural Napa Valley. Here, there are hedgerows and clumps of brush that could afford limited movement to the Wrentits, but the data on breast coloration seem to indicate, as do the data on back coloration, that there is a significant color break between these two localities. Even if the data for the lighter birds from Santa Rosa are combined with those from Oakville there is still a significant discontinuity.

Consideration of these differences and the geographic positions of the localities leads one to conclude that there is the sharpest break in color between the birds so far discussed and those to the east and northeast yet to be mentioned. To be sure the birds from Santa Rosa show considerable overlap with those from northeast of Napa, but there is also considerable distance between the two localities within which is found a population at Oakville that shows much darker color than the population at Napa. There is, however, a significant difference between the birds of Santa Rosa and those to the east from Putah Creek and Knoxville.

From northeast of Napa to Knoxville there is a very even cline toward lightness involving the birds on the Vaca Mountains and along Putah Creek. The Knoxville

birds appear to average the lightest of all samples taken although there is overlap of twice the standard errors with those birds to the south. There is a significant break in color between the birds from north of Healdsburg and those from Knoxville, Putah Creek, and the Vaca Mountains.

The four specimens from Clearlake Park in Lake County average lighter than those from north of Healdsburg and slightly darker than those from Knoxville.

Back color.—The analysis of back coloration was carried out in a manner similar to that used for breast coloration. There is, however, not as wide a range of color expression in the back plumage. These colors may be roughly described as differing values (shades) of dusky brown. Comparison of the specimens with the four color-class standards provided results similar to those for breast coloration. The averages of some localities do not fall exactly into the same sequence as for breast color, but there are

Table 8

Back Coloration

(Light to dark scale—1 to 4)

Locality	Number	Range	Mean and standard error	Standard deviation	Coefficient of variability
Marin County	44	2–4	3.70±0.08	0.51	13.8
Russian River	9	2–4	3.33±0.31	0.87	26.4
NW Healdsburg	12	2–4	3.33±0.20	0.67	20.3
N Healdsburg	22	1–4	2.59±0.16	0.73	28.2
Santa Rosa	11	2–3	2.27±0.15	0.47	20.4
Oakville	14	2–4	2.29±0.17	0.62	27.0
Angwin	4	1	1.00		
NE Napa	16	1–3	1.50±0.16	0.63	42.0
Vaca Mountains	54	1–3	1.68±0.08	0.57	33.5
Putah Creek	58	1–3	1.59±0.08	0.62	38.7
Knoxville	19	1–2	1.53±0.12	0.51	34.0
Clearlake	4	1–2	1.50		

no major differences between the seriations for back and breast color (see figure 3 and table 8). The greatest difference between breast and back gradients occurs in birds of the Oakville and Santa Rosa localities. In breast color the sample from Oakville averages about one color step darker than those from Santa Rosa and north of Healdsburg. In back color the averages for birds of Oakville and Santa Rosa are equivalent and both are lighter than those from north of Healdsburg.

Back color shows no overlap of twice the standard errors of specimens from northwest and north of Healdsburg. In breast color there is no overlap even of the standard deviations.

Specimens from Angwin all appeared to be in the lightest color class. Thus they do not fall in line with the back color cline between north of Healdsburg and northeast of Napa as they do for breast color. However, as mentioned earlier, they were collected in February and are more worn than any of the other specimens used for the color analysis.

The steepened gradient that was mentioned in connection with breast coloration between the last six localities and the first six, is even more obvious here. In back color there is no overlap of twice the standard errors between these two groups. The last five localities show more homogeneity than any other grouping. (The small sample from Angwin is omitted from this discusssion.) There is a step difference of only 0.2 in back

color among their means. In breast color there is a difference of only 0.7 among the means. The birds of these eastern and northeastern localities then appear to be somewhat set apart at the lighter end of the color scales. Since there appears to be correlation between vegetation and Wrentit color, as will be shown later, this break is to be expected since the humid coastal type of vegetation is present interiorward as far as the Napa Valley, with minor exceptions near Angwin and Napa, but it is replaced eastward by the more xeric interior flora with which the lighter birds are associated.

To recapitulate, the darkest Wrentits of those investigated occur along the coast from Marin County to the Russian River region and northeast from there to the area northwest of Healdsburg. These first three localities contain birds that average considerably darker than any others although they are not significantly different from all of them. They are considered taxonomically as belonging to the race *C. f. rufula.*

The next three localities in the geographic sequence outlined harbor birds that lie in the approximate middle of the color span of breast and back. Taxonomically these have been designated the intermediate race *C. f. intermedia.* These Wrentits in turn average darker than those birds found farther east and northeast. In back color this break appears to be statistically significant but more overlap is found in breast coloration.

The birds from Angwin (small sample), Napa, the Vaca Mountains, Putah Creek, Knoxville, and Clearlake (small sample) are all similar and all considerably lighter than other samples to the west. Taxonomically these birds are of the race *C. f. henshawi.* The steepened gradient between these latter samples and those to the west is a reflection perhaps of the partial isolation produced by the agricultural areas between them.

Overall trends are from darkest Wrentits in the west to lightest birds in the east.

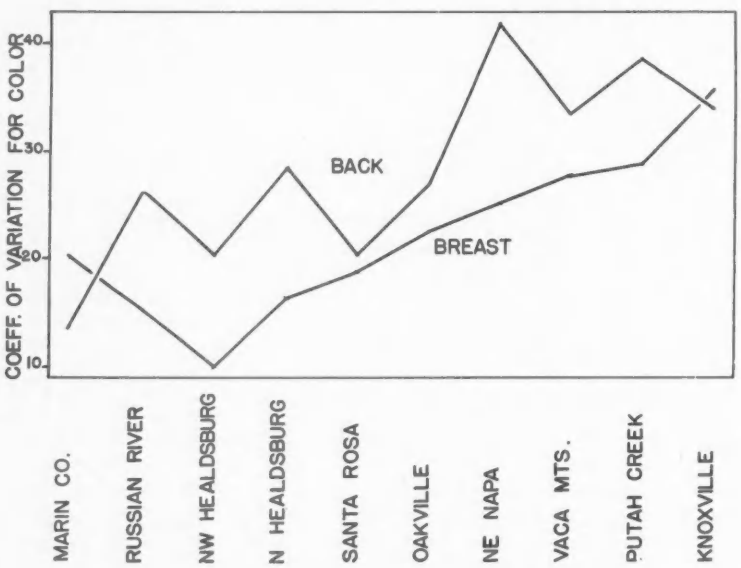

Fig. 4. Coefficients of variation for back and breast coloration.

Pathways between these extremes are not direct but are probably as indicated by the arrows in figure 1.

Color variability.—Variability of coloration is much higher than that of the mensural characters and shows an interesting trend (fig. 4). Generally, the darkest birds have the least variability and the lightest birds show the most. This trend leads one to postulate that the environment which allows selection for the darker plumage is more restrictive or exerts a sharper selection on color expression than the environment in which the lighter birds exist. There is correlation here with weather data, to be discussed later, in which both temperatures and humidities are shown to exhibit wider fluctuations in the interior localities than along the coast. Davis (1951:89) working on *Pipilo aberti* and *P. fuscus* and Selander (1954:79) studying *Chordeiles minor* have found similar situations in which more variable environments contain birds more variable in color than those found in more uniform environments. Pitelka (1951:364) also found population variation and habitat variation to be correlated in *Aphelocoma*.

ANALYSIS OF THE ENVIRONMENT AND CORRELATION WITH PLUMAGE COLORS

COLOR AND ILLUMINATION OF SUBSTRATE

The concept of "substrate" must encompass more of the vertical dimension for brush-inhabiting birds than for ground-dwelling mammals and birds. Hence, it is more complicated to describe this "substrate" and to analyze its color with respect to its possible influence in the selection of color variants in such birds.

The foliage of a tree makes objects under it appear darker by reducing the illumination reaching them. The amount of darkening under a tree depends on the density of the foliage overhead. Hence the measurement of the light reaching the understory beneath different trees gives a measure of the amount of darkening with respect to the open illumination from the sky and thus provides an index for the density of those trees. The fact that Wrentits live in what appear to be variously illuminated areas of chaparral (used loosely here to refer to life form) prompted the measurement of light intensities in several localities.

The assessment of brush density was carried out by using a Weston illumination meter, model number 756, that was built to read directly in foot-candles. The light-sensitive element was covered with a Weston Invercone as an integrating device. The importance of such an addition was pointed out by Wallace (1937). This integrating screen greatly minimizes the effects of the variance of the angle of incidence of light. Experimentation with the present instrument showed likewise that such a filter is indispensable for use under varying sun position, for measuring bright sun flecks beneath the vegetation, and indeed even for measuring the full intensity of the brightest sunlight. The Invercone cuts down the light readings to one-tenth of their value regardless of the actual amount of illumination.

The method used for measuring brush density involved selecting chaparral areas at each of nine localities. Fairly uniform and representative cover in which Wrentits were actually collected or at least seen was desirable. One end of a 100-foot line was tied to a bush, usually in which a Wrentit had been seen, and the cord then was strung out in as nearly a straight line as possible, tightened up, and tied to a bush by its other end. In laying out the line an attempt was made to follow the general direction of the Wrentit as it moved away from the starting bush in order to measure areas of brush that were used by the birds. The cord was marked at five-foot intervals. Light readings were made by placing the light paddle containing the sensitive element at ground level. The sensitive cell was pointed vertically. Readings were taken at five-foot intervals

directly beneath the cord and one foot on each side of the cord. Use of the 100-foot line thus gave 60 recordings arranged in a regular pattern throughout the irregularly placed chaparral plants.

The validity of the transect method for plant censusing was tested by Bauer (1943). His system yielded, in a fraction of the time, information which was comparable to forestry service records that contained actual tallies of the plants over whole plots. The transect method used here for light recording is an adaptation of the same basic idea. My transects utilized for density measurement were at the same time used as species census lines.

Light readings obtained beneath the brush have been expressed as percentages of the overhead unobstructed light. It is assumed, although not proven, that plant canopies remove the same percentage of light regardless of the level of the overhead intensity. Thus the percentages become indices of brush density which can be compared roughly under the various illumination characteristics of the sky. Measurements were never made before 9:00 a.m. or after 3:00 p.m., Pacific standard time. If the sun was more than 45 degrees from the zenith no measurements were made.

Possible differences in spectral transmission of the leaves of various species of plants have been disregarded. The visual apparatus of vertebrate predators is relatively insensitive to such qualitative differences in sunlight and only the quantitative sum of whatever light is present is considered of importance. With minor exceptions, the response of the light meter is uniform over the visual range.

The color value of the area under the brush is also produced or effected importantly by a combination of factors other than the amount of visible illumination reaching it. In denser brush, for example, where less evaporating sunlight strikes the ground, there is greater moisture retention resulting in simply making objects appear darker because they are wet. Also, moisture aids the production of dark humus. Moreover there is less bleaching effect of direct sunlight. All these factors contribute to a darker soil surface and the converse effects in less dense brush can be outlined to partly explain the lighter substrate to be found there.

Since animals tend to match the color values of their surroundings, then the darkest habitat should contain the darkest Wrentits and the lightest should harbor the lightest colored birds. The graph of light transmittance (fig. 5) shows the results of the recordings. The localities are arranged to correspond with the breast color seriation from the darkest end of the gradient. It will be seen that the overall trends are somewhat as predicted. The readings from Russian River indicate more dense brush than in Marin County, which inverts the relationship to the coloration of the Wrentits. However, the presence of an overstory or at least bordering individuals of redwood, laurel, and Douglas fir at Russian River may explain the low illumination found there at ground level.

It is of interest that in the study area any sequence of localities from southwest to east or northeast shows decreasing or equal brush density as measured by light transmittance. Likewise any sequence running from the northwest to the east or southeast shows equal or decreasing brush density. The same directional seriations show up in breast and back coloration from dark to light colors. It is also of interest that the measurements for the extreme localities, with respect to east and west, are considerably different.

Estimates of the average vertical thickness of the leafy canopy above the transect lines were made in conjunction with the amount of representation of each plant species along these lines. Multiplication of this vertical thickness by the linear footage gives a vertical area of canopy which is an index of the amount of living space available to the Wrentits, since they spend nearly all of their time within this foliage layer. Summation

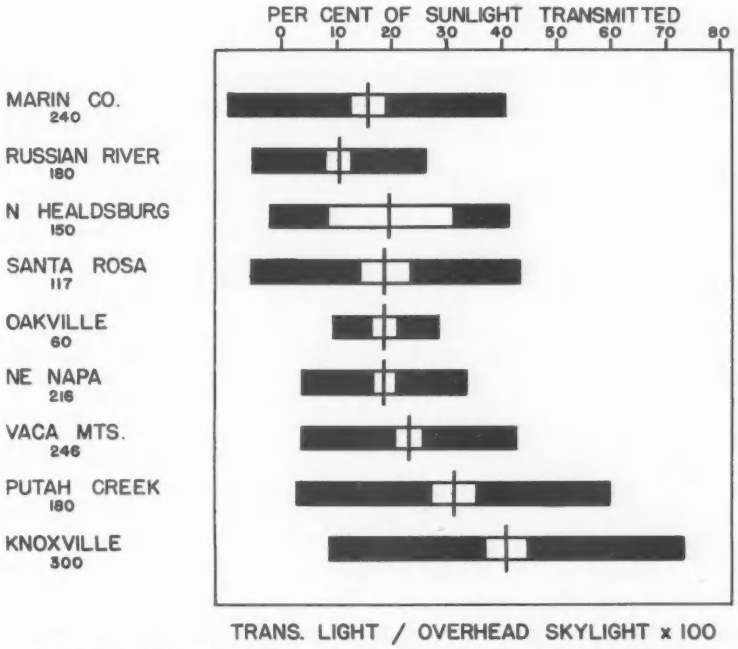

Fig. 5. Bar graphs showing the percentages of skylight transmitted through the chaparral canopies. Higher transmittance occurs through less dense brush and lower transmittance occurs through denser brush. Means, standard errors, and standard deviations as in figure 3.

of these vertical areas allows the calculation of the average number of square feet of vertical area per linear foot of transect for each locality. The results of these calculations are found in table 9.

By comparing these figures with the data for light transmittance, it can be seen that the more objective measurement of density by means of light measurement agrees generally with this somewhat subjective estimate of canopy thickness. The correlation coefficient r is + .698 for light transmittance and canopy thickness. The thickest foliage layer appears to occur in Marin County. The light readings at Russian River were reduced by surrounding trees, but since these trees were not directly above the transects they did not add to the estimates of canopy thickness. Thus, brush density indicated

Table 9

Average Vertical Area of Living Space

Locality	Vertical area per linear foot	Locality	Vertical area per linear foot
Marin County	3.69	NE Napa	2.46
Russian River	3.24	Vaca Mountains	3.29
N Healdsburg	2.80	Putah Creek	2.08
Santa Rosa	2.65	Knoxville	1.86
Oakville	2.65		

by the vertical area figures is not greater than that in Marin County in the way the light readings seem to indicate. One exception, that of the Vaca Mountains, may be explained by suggesting that the canopy there, while almost as thick vertically as that at Marin County, is nevertheless sparse enough to have allowed light readings to be much higher than those at the coast. Disregarding this one exception, the data for vertical area indicate good correspondence with density measurement by light readings and with the color gradient of the Wrentits.

Another aspect of the coloration of the "substrate" is the actual color of plant parts, especially those close to the color of the Wrentits and which provide part of the backdrop against which the birds would be seen. Stems of plants most commonly present were collected from Marin County and the Vaca Mountains for a rough color determination. These are shown in table 10 and are presented in order of abundance as represented by the transect data.

Generally speaking, the lightest Wrentits are quite gray in breast coloration. The darkest birds are deep ruddy-brown. The grays of the stems listed most closely approximate the color of the lightest birds, such as those from the Vaca Mountains, while the

Table 10

Color of Stems of Plants in Two Regions

MARIN COUNTY

Genus	Stem color	Per cent
Ceanothus	dark gray	51.0
Pinus	gray	10.7
Baccharis	gray	9.3
Polystichum	brown	5.8
Arctostaphylos	dark red-brown	5.7
Vaccinium	reddish brown	5.0
Rubus	red-green	4.1
Myrica	gray	2.3
Arbutus	dark red-brown	1.8
Rhamnus	gray	1.5
Pteris	brown	1.3
Corylus	brown	.4
Lonicera	red-brown	.3
Diplacus	brown	.2
Rhus	gray	.2

Totals: gray 75.0 per cent; 6 species
brown 20.5 per cent; 8 species

VACA MOUNTAINS

Quercus	gray	30.8
Adenostoma	gray	26.7
Arctostaphylos	dark red-brown	9.1
Photinia	gray	7.8
Cercocarpus	gray	5.0
Garrya	gray	4.7
Ceanothus	gray	4.5
Rhus	gray	4.1
Umbellularia	gray	3.3
Diplacus	brown	1.4

Totals: gray 86.9 per cent; 8 species
brown 10.5 per cent; 2 species

red-browns are closest to the darkest birds as, for instance, those from Marin County. The higher overall percentage of browns and red-browns in plant parts plus the presence of more species with brown bark in Marin County suggest another factor besides density of the brush and its related effects that may influence the substrate color.

All these factors, denser brush, slower evaporation of soil moisture, more humus production, less bleaching of leaf litter, and more dark stems, contribute to darker habitats. Such conditions are found along the coast where weather factors, the details of which are presented later, may be expected to produce heavier vegetation.

CHAPARRAL COMPOSITION

The percentage occurrences and constellations of plant species found at each locality provide clues concerning some aspects of the color distribution of the birds. For example, the abundance of *Adenostoma fasciculatum* (fig. 6) shows a striking correlation with breast coloration. The darkest birds are found where *Adenostoma* is scarce and lighter birds are found where this plant is abundant. Possibly the "substrate" color determined by the *Adenostoma* is one cause of the relationship here. The discussion of Davis (1951: 41) concerning the terms "black chaparral" as applied to *Adenostoma* and "blue chaparral" referring to *Ceanothus* appears not to explain color correlations as well for the Wrentit as for the Brown Towhees since the lightest Wrentits occur where "black chaparral" is most abundant and the darkest are found where "blue chaparral" is most common.

Rhus diversiloba occurs widely and contributes to Wrentit habitat and food supply. This more vine-like plant appears least in the transects where both the extremes of Wrentit color are found and occurs most in those areas where Wrentits are medium in darkness. *Diplacus aurantiacus* shows a similar pattern of occurrence, but apparently it does not contribute appreciably to the living areas of the birds.

Species of *Quercus*, called scrub oak because of their life form, are present in most localities and provide much of the habitat for the Wrentits. The fact that one species of oak does not occur all across the region is an indication of differing environmental conditions. *Quercus wislizenii* is more abundant where Wrentits are darker in color; *Q. dumosa* is more prevalent where Wrentits are intermediate or lightest; *Q. durata* is present mainly where the birds are the lightest.

The picture for *Ceanothus* and *Arctostaphylos* is somewhat more complex. First of all, these two genera are difficult ones taxonomically, and second, the region is sprinkled with several different species of each genus, a further indication of differing conditions. There are great numbers of large-sized plants of *Ceanothus thyrsiflorus* in Marin County and at Russian River. Here this species makes thick canopies and provides dense cover utilized widely by Wrentits. Other species of the genus, although present at all other localities sampled, do not represent as large a percentage of the total vegetation. *Ceanothus cuneatus*, a plant living in dry situations, occurs in only three localities, Oakville, Vaca Mountains, and Putah Creek. In all of these areas Wrentits are intermediate or light. *Ceanothus cuneatus* is present on extremely dry south-facing slopes near Healdsburg, but it did not appear in the transect data.

Arctostaphylos occurs in the transects of seven of the nine localities. At least six different species are represented. At Napa, two species, *A. canescens* and *A. stanfordiana*, grow intermingled to produce sizable, almost pure stands. *Arctostaphylos viscida* comprises similar nearly pure patches in the chaparral at Knoxville. Even though these stands are relatively barren at ground level, Wrentits use them considerably. *Arctostaphylos glandulosa* occurs at the station north of Healdsburg and in the Vaca Mountains. Apparently no other localities share a common species. Manzanitas often grow as isolated individuals and thus may not have been sampled completely.

Umbellularia californica is present in the transects of six localities, but no particular pattern of occurrence appears to correlate with the color trends of the Wrentits.

Arbutus menziesii is present only in the transects in Marin County and at the Russian River; these localities contain the darkest birds. One Wrentit from north of Healds-

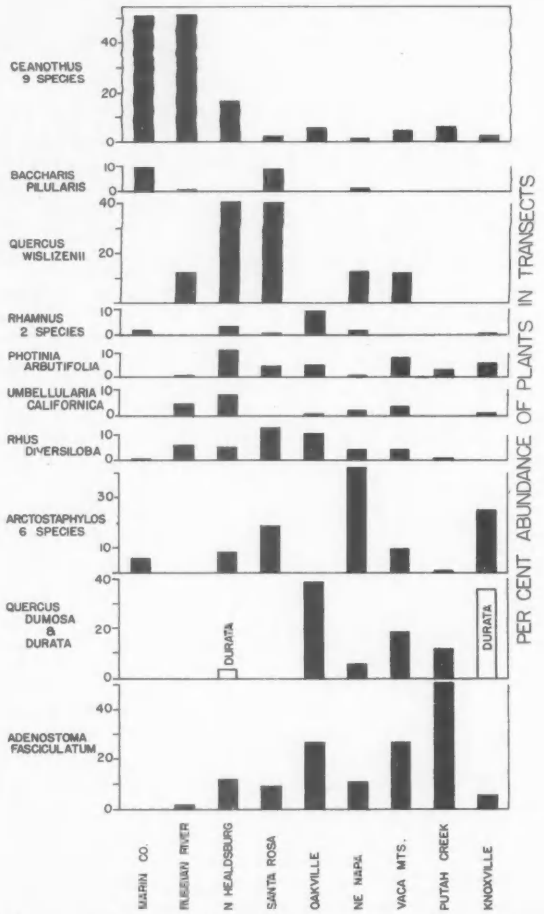

Fig. 6. Histograms showing percentages of the most common plants at nine localities. Species of *Ceanothus, Rhamnus,* and *Arctostaphylos* have been combined only for simplicity of graphing.

burg was taken from madrone although this plant species did not appear in the transects from there. *Arbutus menziesii* is too large and open to be considered a typical chaparral plant. It is most often found in moist areas that also support redwood and Douglas fir trees.

Bracken fern (*Pteris aquilina*) is present in transects at Marin County, north of

Healdsburg, and Santa Rosa. These areas have the darkest and intermediate birds. *Myrica californica* and *Vaccinium ovatum* occur only in Marin County and here provide much used plant food and cover. These plants are most common under the Bishop pine forest and are not widespread in the actual chaparral formation. *Gaultheria shallon* also occurs only in Marin County, but it is a low shrub probably not offering much available living space to the Wrentits.

Rhamnus californica is present in the transects of six localities but represents less than eight per cent in any of them. Wrentits were taken from this species only in the Vaca Mountains where no transect records for the plant occur. *Rhamnus crocea* also occurs in small percentages along Dry Creek near Oakville and northeast of Napa but was encountered at no other locality.

Cercocarpus betuloides appears in the transects north of Healdsburg, Oakville, and the Vaca Mountains. Birds were taken from this species at Oakville, northeast of Napa, and the Vaca Mountains. It grows in rather arid situations although it was not found in abundance.

Garrya fremontii occurs in amounts of less than five per cent at Santa Rosa, Vaca Mountains, and Knoxville but nowhere were Wrentits taken from this species.

Photinia arbutifolia is present at all localities although over ten per cent only at the station north of Healdsburg. It appears to be rather tolerant of environmental conditions since it is so widespread in distribution. Wrentits were taken from this species at six localities. One-third of the specimens from Putah Creek, 19 birds, were taken from *Photinia*. There, these plants filled a dry draw that was surrounded by grassland. These harbored a number of Wrentits in the fall when the red holly berries were being eaten by the birds. Such isolated pockets of habitat were not sampled by transect but did add to the specimen collection.

Baccharis pilularis seems to be confined to fairly moist areas. It was found at Marin County, Russian River, Santa Rosa and northeast of Napa. Wrentits were taken from this plant north of Healdsburg, although it did not appear in the transects there.

A few other plants were encountered at various localities but were not important constituents of the chaparral. Figure 7 summarizes the abundance of the most common plants for six of the localities.

PLANTS FROM WHICH WRENTITS WERE COLLECTED

Records were made of the plant species from which the 267 specimens of Wrentits were collected. With the exception of 32 birds (12 per cent), all Wrentits were taken from plants that appeared in their respective local transects. These exceptions were from relatively rare plants, specialized spots such as fence rows and stream banks, or from plants on the edges of the main chaparral which were not considered as typical of the overall cover type. The degree to which transect sampling of plant species agrees with cover use, as indicated by the plants from which the birds were taken, is shown in the accompanying graphs, figure 7. The plant species are given in per cent of the total transect footage covered at each locality, and the number of birds shot in each plant species is shown as the per cent of the total birds taken from that particular locality. Some obvious parallels occur.

Species of *Ceanothus* are present at all localities and in some measure the number of Wrentits collected from these plants shows a correlation with the linear amount of *Ceanothus* intersected by the transects.

Thus at Marin County and Russian River where *Ceanothus* makes up 50 per cent of the transect tallies, the number of birds taken from plants of this genus makes up almost a third of the birds from each of these localities. At Napa, where species of

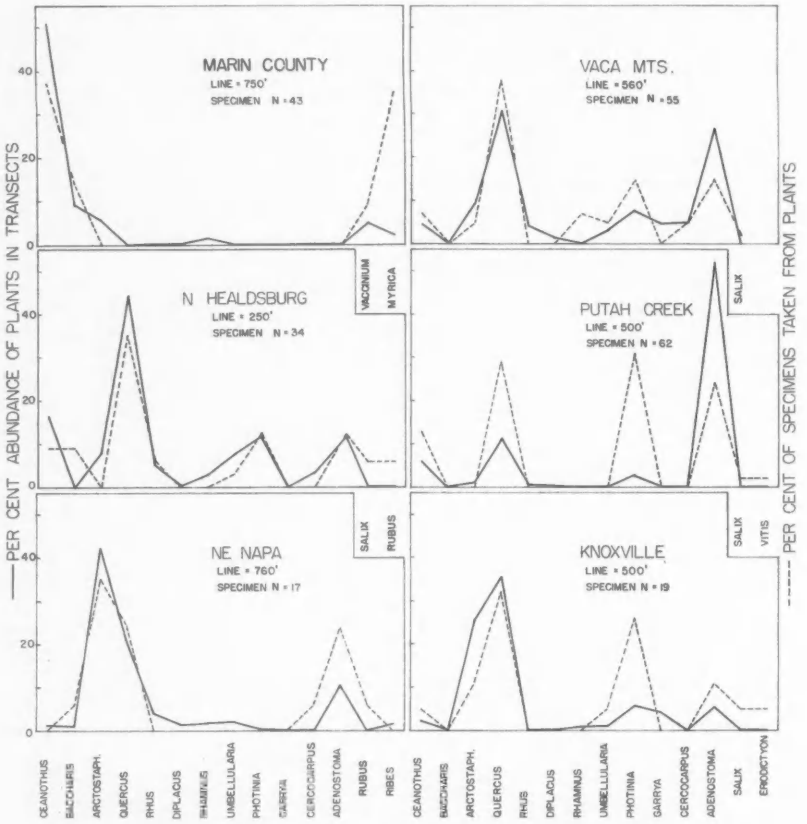

Fig. 7. Graphs representing percentages of plant abundance (solid lines) and the percentages of Wrentits taken from these plants (dashed lines). The plants listed are those most commonly encountered at these localities.

Ceanothus comprise less than three per cent of the lines, no birds were taken from these species. At Knoxville where again *Ceanothus* is present along less than three per cent of the transect lengths, only one bird (5 per cent) was taken from a plant of this genus.

A similar analysis may be made for the several species of scrub oak, *Quercus* sp., which make up considerable portions of the transect data from most of the localities. At the station north of Healdsburg 44 per cent of the line lengths intersected scrub oak and 35 per cent of the birds from this locality were taken in scrub oak. The station northeast of Napa, the Vaca Mountains, and Knoxville all have large percentages of scrub oak and likewise have high percentages of bird collections from this group of plants.

Further correlations may be made for *Adenostoma* especially and for *Photinia* and species of *Arctostaphylos*.

Since collecting of specimens is of a random nature, all these coincident peaks suggest that fairly representative habitat composition figures with respect to Wrentit usage

have been obtained. Of course the birds move rapidly from one species to another where there is interspersion of plant kinds.

CLIMATE

Most weather data for California are collected at stations operated by or in cooperation with the United States Weather Bureau, and the data are gathered to give macroclimatic descriptions only. Stations more advantageously placed and operated by a biological investigator would have the disadvantage of being short-term sampling stations. The annual summary of 1952 of "Climatological Data, California section," provides records for the areas concerned in the present study that represent up to half a century of compilation. Here are to be found normal monthly temperature and precipitation figures for eleven stations that lie within or close to the borders of the region investigated. The relevance of averages of temperature and rainfall might be questioned, since it is likely that extremes are more important in influencing biological adaptations. However, mean figures will allow comparisons between different localities that may bring out important environmental trends.

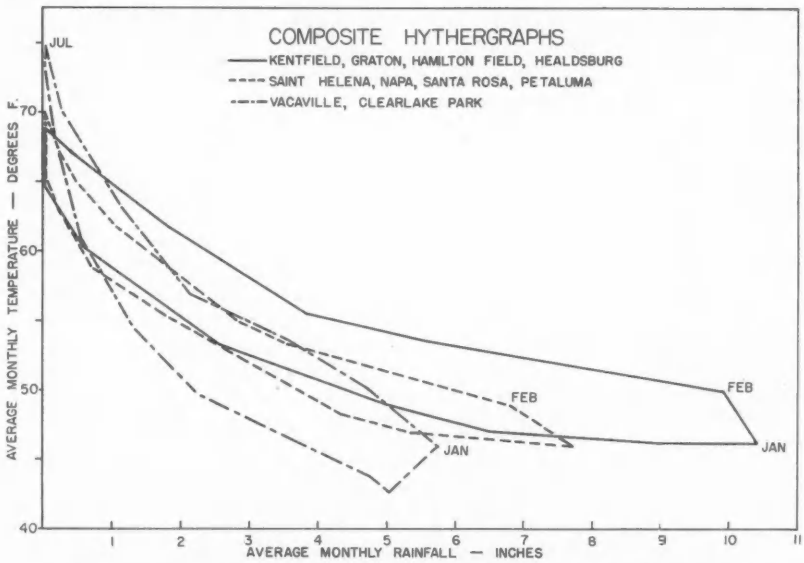

Fig. 8. Composite hythergraphs from United States Weather Bureau data. Solid line represents area in which darkest Wrentits are found; dashed line, area in which intermediate birds are located; dot-dashed line, area in which lightest birds exist.

Hythergraphs for the eleven weather stations were constructed by plotting the normal monthly temperature against the normal monthly rainfall. By connecting these points from January through the months and back to January there is produced a twelve-sided polygon representing some of the aspects of climate for that locality. Larger areas can be roughly compared by circumscribing several polygons for neighboring stations with a line that now describes these aspects of climate for the region included between the separate localities, provided the distance between them is not excessive.

For the present study, hythergraph polygons were circumscribed for the weather

stations at Kentfield and Hamilton Field in Marin County, together with those at Graton and Healdsburg in Sonoma County. These stations represent the coastal region in which the darkest Wrentits are found. Polygons for stations at Santa Rosa and Petaluma in Sonoma County and Saint Helena and Napa State Hospital in Napa County were included in a regional representation for the area in which intermediate Wrentits exist. For the region farthest inland containing the lightest Wrentits, polygons for Vacaville in Solano County and Clearlake Park in Lake County were combined.

The following points may be made from a consideration of the three composite hythergraphs shown in figure 8. Rainfall is heaviest during the winter months in the coastal region, moderate in the region of intermediate breast color, and least in the inland region. Summer precipitation provides no differentiation of the areas since there is practically no rain during this season at any of these stations. Winter temperatures average highest in the coastal region, moderate in the intermediate area, and lowest inland. Summer temperatures are lowest along the coast, moderate in the intermediate region, and highest interiorward.

Further search into the available data of the United States Weather Bureau revealed that beginning in 1930 there were sporadically published summarizations of various aspects of California climate in the form of state outline maps with isometers of these weather factors drawn over the surface. Portions of these isometers were enlarged by the author on maps of the region under consideration by using grid lines on a transparent overlay. These maps were evidently drawn originally in a general manner since the Weather Bureau is limited by a lack of stations. Interpolations between the existing stations may thus be inaccurate, but the overall trends should be present. Relative humidity isometers are drawn at ten per cent intervals, temperatures are shown at five degree intervals, and the average number of clear and cloudy days per year are given in 25 and 20 day intervals, respectively. For each of the 12 collecting localities, measures for the various climatic factors were taken from these maps using the value of the whole interval, within which the locality is situated, as the statistic. Where an area fell close enough to an isometer to place its accuracy in doubt, both intervals on either side of the line in question were used as the figure for that locality. These data were tabulated for the collecting localities in the same order as that used in the color seriation of the Wrentits, beginning at the dark end of the gradient.

Cloudiness and fog.—Cloudiness greatly reduces the evaporative and bleaching

Table 11

Average Number of Totally Cloudy Days and Totally Clear Days Per Year and Annual Range of Mean Temperature

Locality	Cloudy days	Clear days	Range of mean temperature (F.)
Marin County	120–140	150–175	10–15
Russian River	80–120	175–200	15–20
NW Healdsburg	60–80	200–225	25–30
N Healdsburg	60–80	200–225	25–30
Santa Rosa	80–100	225–250	20–25
Oakville	60–80	250–275	20–25
Angwin	60–80	250–275	25–30
NE Napa	40–60	250–275	15–20
Vaca Mountains	40–60	225–250	20–25
Putah Creek	60–80	225–250	25–30
Knoxville	80–100	225–250	30–35
Clearlake	60–80	225–250	30–35

radiation that reaches the earth. Since, as mentioned earlier, the amount of moisture retained at ground level has an effect on humus production, and the amount of direct sunlight has an effect on the color of leaf litter via bleaching, wherever the incidence of a cloud cover or fog is high, one would expect to find darker soils and soil coverings than where the skies are more commonly clear.

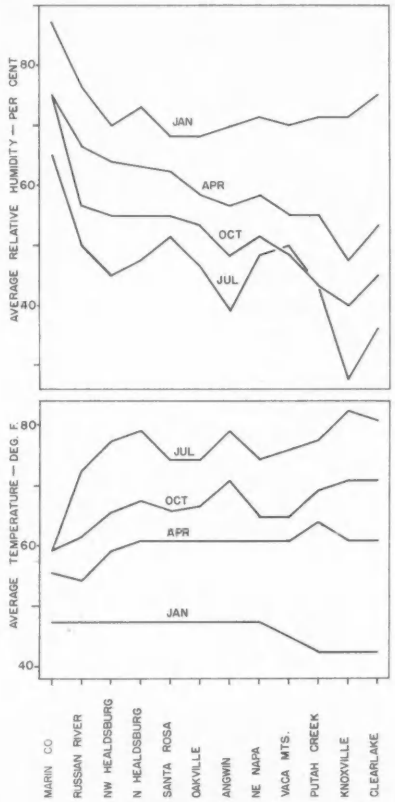

Fig. 9. Summary of average relative humidities and temperatures for four months showing inverse relationship of these weather factors.

From an inspection of table 11 showing the number of clear and cloudy days per year for the various collecting localities, it can be seen that the general trend is somewhat as expected, namely that along the coast there is more cloudiness and fog while inland there are more days that are clear.

Temperature.—Temperatures are treated in the maps of the Weather Bureau for only four months of the year but they may be considered as representative quarterly statements. Mean maxima, means, and mean minima of temperature for January, April, July, and October are available. From these midpoints in the readings were plotted and are summarized in figure 9. Note especially the data for July which show increasing

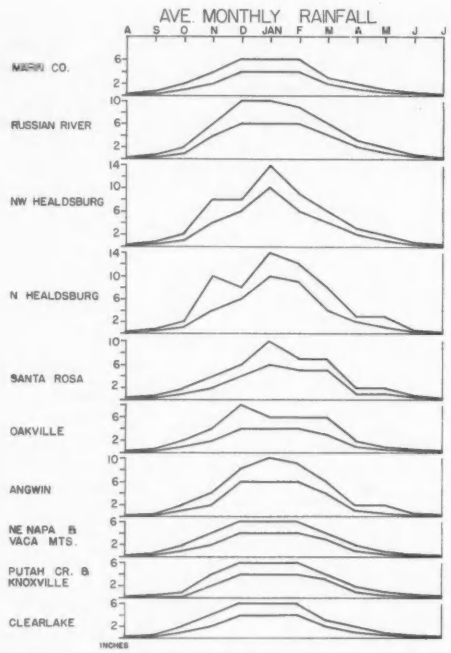

Fig. 10. Graphs showing average monthly rainfall for the collecting localities.

temperatures inland where less dense brush and lighter birds are found. The effect of thermal energy, expressed here as temperature, on evaporation is well known. Where temperatures are consistently low, we would expect less evaporation of soil moisture than in regions of seasonally higher temperatures and the interpretation concerning the effects of this on substrate color may here again be brought out.

Table 11 gives records taken from a map showing the annual range of mean temperatures. These ranges correspond more closely to roughly concentric rings with their centers in Marin County than to the sequence of localities indicated by the studies of breast coloration. This does show, however, that the darkest birds, which are less variable in color, exist where yearly fluctuations in mean temperature are least and that the lightest birds, which show more variation in color, exist where such fluctuations are greatest.

Relative humidity.—As shown in figure 9, average humidities tend to be higher toward the darker end of the color cline along the coast and lower toward the lighter end inland. While relative humidity may not be as useful as vapor pressure deficit in ecological studies, still these data lend their support to the idea of lower soil moisture evaporation along the coast and greater water loss from the litter farther interiorward.

Precipitation.—It might be supposed that Marin County would receive the largest amounts of rainfall in keeping with its comparatively high humidity values. However, this is not true. In fact figures for Marin County are almost equivalent to those for Napa and the Vaca Mountains (see fig. 10). Other factors in this coastal region then

must be sought to explain the humidity levels found there. Proximity to the sea and Tomales Bay is of course a major factor for several reasons. Temperatures in Marin County are consistently rather low because of the nearness of the cold sea water, associated with which are rather high relative humidities. On shore ocean breezes are laden with moisture and are generally more uniform in temperature than terrestrial winds. Coastal fogs and cloudiness likewise prevent solar warming of the area to some extent and in addition hinder evaporation of the surface moisture.

Rainfall in the Healdsburg region according to these maps has almost the highest value of any of the localities for some months. Yet the vegetation there has more the aspect of the arid areas farther east than that of the humid coastal zone along the western portion of Russian River and in Marin County. Healdsburg is of course farther inland than are these latter stations. It should be mentioned that temperatures at Healdsburg average somewhat higher in the summer than for the other collecting localities nearby. It is possible that these comparatively high fire-season temperatures have encouraged more frequent burning of the chaparral in spite of high annual rainfall and thus have hindered more complete regrowth to denser successional stages. Indeed, there are fire-scarred areas evident over large sections of the hills between Healdsburg and Mercuryville to the northeast. The more frequent burning of the plant cover in areas of low summer humidity and high temperature, irrespective of precipitation levels, represents a way in which the brush density is kept lower than in more moist, cooler regions where fire expectation is lower.

DISCUSSION

In the course of describing climate and the plant matrix we have brought out the variations in the color of Wrentits that correlate with variations in some features of the environment. These correlations of course are not to be construed as demonstrating causal relations between climate and color. Gloger's rule, unfortunately, is usually worded in such a way that causality may be inferred from its statement that dark-colored organisms are to be found in humid areas, whereas lighter-colored animals of the same species live in arid areas. There is no mention of any agency or mechanism interposed between humidity and the animals.

We may then analyze possible indirect connections between climate and avian coloration. First, there is a direct relationship between moisture and plant growth that hardly needs documentation. Fairly adequate statements can also be made regarding the influence of humidity on plant density. On the other hand, the effects of the plant cover on humidity are not so well known, but to a degree there is an influence in the sense that humidities are bound to be higher where more plant material is present to absorb from the soil and to release into the air by transpiration the water resources of that soil.

The effects of temperature on transpiration rates and soil desiccation are of course considerable. The correlation of high temperatures with low humidities and the reverse have been pointed out. These connections are most obvious for summer when moisture relations are the most critical for many plant species.

The sparsest chaparral, which occurs at the interiormost localities, very likely has suffered the greatest frequency of burning, since in this region, summer temperatures are highest and humidities are lowest. It is only through long periods free from fire in conjunction with better environmental conditions for growth that the establishment of heavier vegetation is possible, as along the coast.

The darkening effect of moisture on soil color is well known. The habitat for the birds may be effectively darkened by dark and/or moist soil and moist soil may be likewise rich in humus which also has a darkening influence.

In sparse brush, where more sunlight can penetrate to the lower plant and soil levels,

there is more lightening of colors by bleaching than in more dense brush. This, correlating with the moisture relations just described, adds another factor in the production of lighter and darker habitats in the various areas.

We now have a reasonable set of correlations that point to the causative mechanism underlying Gloger's rule. The climate has direct effects on the plant matrix, producing different colored substrates in different climatic areas. More specifically, in temperate regions with relatively high humidity, low temperature, and frequent cloudiness, the plants respond by growing luxuriantly; this in turn allows the production of dark, moist soils with abundant humus that is more nearly screened from the bleaching action of the sun than in other situations. Through the agency of natural selection, then, the darker colors of Wrentits in time would be favored and the birds come to match the surroundings in this dark habitat.

The habitat itself, controlled by climate, shows a gradient of structure and density which could afford a graded selective action on the Wrentits. Natural selection is thus the most obvious agent that has caused the differentiation of colors and has enhanced the success and survival of the Wrentits in the differing environments.

SUMMARY

Several types of measurable variation were considered in this study of correlation of the attributes of Wrentits with environments in a west-east transect in central California. It is concluded that linear measurements have their greatest meaning if expressed in terms of body size, represented as weights.

The Wrentits measured fit closely Allen's rule in that they show lengthening of extremities in warm climates.

Bergmann's rule, which reflects an inverse relationship between environmental temperatures and body mass, also is evident in these birds.

There is a steep color gradient over a relatively short geographic range in the back plumage and even more strikingly in the breast plumage of these Wrentits. It can be generally stated that the darker birds inhabit the coastal region and that toward the east, interiorward, the birds become progressively lighter.

The darker birds exhibit less individual variability in coloration than do the lighter birds. This is correlated with less variation in the climatic factors present where the darker birds live and more variation of climate where the lighter Wrentits occur.

The composition of the habitat of the Wrentit, in terms of plant species was sampled using line transects. Some kinds of plants show distributions parallel to climatic gradients and gradients in plumage coloration. Such plants are common at one end of a color cline and tend to disappear toward the other end.

The brush, analyzed in several ways, shows greater density along the coast where this is encouraged by high humidity and low temperatures in conjunction with frequent cloudiness and fog. Interiorward, the brush is less dense because of less moisture and higher temperatures, and there are more cloud-free days per year. Because of conditions more favorable for summer fire in the interior, it is expected that there would have been more frequent burning of the chaparral and thus maintenance of more sparse brush there.

A simple investigation of stem colors has shown more plant species with dark brown stems, as well as a higher representation of these plants, in the western part of the area. Fewer dark brown-stemmed species and lower representation of these is to be found in the eastern areas.

The denser brush possesses a darker living area within it by virtue of higher moisture

retention which imparts darker colors to the lower parts of the habitat, encourages greater humus production, and offers better screening of soil litter from the bleaching action of the sunlight. The sparser brush in the east has a lighter living area within it by virtue of lower moisture retention which makes objects appear lighter, inhibits humus production, and provides less screening of soil litter from bleaching.

It has been shown that there is, in fact, good correlation between the color gradient of the Wrentits and several gradients of the physical and biotic environment. This allows a specific expression of Gloger's rule: Where there is high humidity accompanied by other climatic factors which produce dense chaparral, the habitat is dark in color, and there are to be found in it dark-colored Wrentits. Conversely, where humidities are low and in connection with other climatic factors only sparse chaparral develops, the habitat is light in color and there light-colored Wrentits occur. The advantageous matching of light birds with a light environment and of dark birds with a dark environment has in all probability been produced by natural selection.

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Museum of Vertebrate Zoology, Berkeley, California, June 1, 1959.

A BLACKISH RACE OF THE GRAY SEEDEATER OF NORTHERN SOUTH AMERICA

By ALDEN H. MILLER

The Gray Seedeater (*Sporophila intermedia*) occurs across northern South America from the Pacific slopes of Colombia east through Venezuela to the border area with Guiana and to Trinidad. De Schauensee in his review of the genus *Sporophila* (Proc. Acad. Nat. Sci. Phila., 114, 1952:153–196) has nicely clarified the characters of this species and particularly the separation of it on bill, foot, and mensural characters (pp. 163–164) from the very similar appearing *Sporophila schistacea* which has a geographic range extensively coincident with that of *intermedia*.

Geographic variation within the species *intermedia* has been described by Gilliard (Auk, 63, 1946:570–574) and by de Schauensee (*op. cit.* and Proc. Acad. Nat. Sci. Phila., 99, 1947:121). As a consequence four races have been proposed: *S. i. insularis* Gilliard of Trinidad, the nominate *S. i. intermedia* Cabanis of Venezuela and the northern coast of Colombia, *S. i. bogotensis* Gilliard of the Dagua Valley and upper Cauca Valley of Colombia, and *S. i. agustini* de Schauensee of the upper Magdalena Valley of Colombia. De Schauensee (*op. cit.*, 1952) does not support the separation of *insularis*, the sole distinguishing character claimed for it being the presence of whitish postauricular patches in males; this is a character that is variable individually, as well as racially in the species, and no attempt has been made by me to evaluate the constancy of separation of *insularis* by this means. The white patches are usually absent in *S. i. intermedia*. *S. i. bogotensis* is a darker race than *S. i. intermedia*, and *agustini* is claimed to be paler than *S. i. intermedia* by de Schauensee (1952). Both *bogotensis* and *agustini* have well marked white neck patches. The material of *agustini* that I have seen is not paler than *S. i. intermedia*; however, the separation of this race is doubtless valid on the combination of characters originally ascribed to it by de Schauensee (1947).

The geographic variation across the east-west range of *Sporophila intermedia* known to this point may be summarized, then, as consisting of greater and more consistent development of white neck patches in males at the eastern and western ends of the range, increase in depth of gray in the western extremity in the mountains, and persistence of pale gray in the upper Magdalena Valley coupled with the presence of neck patches. The differentiation in values of the gray of males is generally slight but quite in keeping with that found in many geographic races of birds. Accordingly it was distinctly surprising to find that in the lower humid tropics on the Pacific coast of Colombia a strikingly blackish representative of the species occurs. This form is so much darker than most *bogotensis* that doubt was entertained for some time that it belonged to the same species. However, this Pacific tropical form has all the essential features of *Sporophila intermedia*, especially in contradistinction to *Sporophila schistacea* of this same district, namely, deep maxilla (4.0–4.5 mm.), wing less than 60 mm., dark-colored nails, and relatively long tarsus. Not only is this coastal race darker but it shows more patterning contrast about the head than do other members of the species. Moreover, the pale belly is set off more distinctly. This race may be known as

Sporophila intermedia anchicayae new subspecies

Type.—Adult male, no. 139077 Mus. Vert. Zool., taken on Río Anchicayá, 950 feet, Valle, Colombia, on April 25,1958, by A. H. Miller; weight 12.0 gm.; testis 6 mm. long; original no. 9872.

Diagnosis.—Male differs from *S. i. bogotensis* in blackish rather than gray upper parts (Blackish Slate rather than Deep Neutral Gray of Ridgway). Light neck patches purer white. White and light gray of throat developed as chin stripe, extending along malar regions and joining medially to encircle

Fig. 1. *Sporophila intermedia anchicayae*. Drawing by Gene M. Christman.

gray chin area (see fig. 1). Belly and under tail coverts more extensively white and more sharply contrasted with dark neutral gray of breast. Rump area with a few white-tipped feathers rather than uniform gray.

Range.—Tropical Zone of the Pacific coast of Colombia. Thus far known only from the valley of the Río Anchicayá, where it ranges up to at least 1500 feet elevation.

This new seedeater was first encountered at the type locality which is approximately 40 kilometers southeast of Buenaventura on the Río Anchicayá. Here on April 25 in the cleared edge of the highway on a brushy knoll a male and female were taken in close proximity; probably they were a pair. The male was singing and had fully enlarged testes. The female had an ovum 1½ mm. in diameter and was judged to be approaching breeding state; she obviously had not yet laid. Another adult male was taken at the 1500-foot level in the river valley on December 27; testis 6 mm., weight 11.4 gm. It was in a grassy tangle in an orchard. A fourth specimen, a female, probably of this form, was taken at 3200 feet in a clearing. Since the females of this species show little or no racial differentiation, this fourth bird cannot critically contribute to our knowledge of the range and characters of *anchicayae* although on the basis of geographic and zonal considerations it may best be referred to it.

The adult male from the 1500-foot level is slightly less dark than the type but it has a broader white collar and more white flecking on the rump. The bill color of the males shows some of the yellow characteristic of the species but in the type this is confined to the median area of the mandible and in the other adult male it is developed only on the mandible and in median longitudinal streaks on the maxilla. *Anchicayae* will probably prove to have a general reduction of yellow on the bill compared to other races; this character apparently has some individual, and perhaps age, variation. The female from the type locality has only a trace of yellow on the mandible. The female from 3200 feet, however, shows only slightly less yellow than the male from 1500 feet. Females of the species generally have less completely and consistently yellow bills than males.

The plumage of the topotypic female is a more vivid, intense green above and below than any females of *bogotensis* I have seen. The female from 3200 feet is grayer and does not show this difference. Apparently in this species grayer and more yellowish variants can occur in females of the same population. It is probable, however, that females of *anchicayae* at low zonal levels are darker and more greenish than in *bogotensis* although this is far from an established fact because of the limited material at hand.

Measurements of *anchicayae* do not seem to show any differences from those of the other races. For record purposes, in relation especially to species allocation, the dimensions of the specimens of *anchicayae* are:

	Wing	Tail	Maxillary depth at nostril	Tarsus
♂ type, 139077	55.0	47.8	4.0	15.2
♂ 139079	56.9	47.6	4.5	15.2
♀ topotype 139078	54.3	42.3	4.1	16.1
♀ 3200-foot level, 139080	55.6	47.4	4.2	15.3

The west slopes of the Andes east of Buenaventura rise rapidly and in the Dagua Valley near the crest a comparatively dry area occurs protected from the humid air masses of the coast by an intervening northwesterly directed spur ridge. This situation was clearly described by Chapman (Bull. Am. Mus. Nat. Hist., 36, 1917:21–24) from his early field work in this area. The Gray Seedeaters of this semiarid valley formed the basis for Gilliard's description of *bogotensis*, the type having been selected from Lomitas. This locality, although described as in the humid forest of the Subtropical Zone, is in fact not as humid as this would imply and is vastly less warm and moist than the tropical areas along the Río Anchicayá west of the spur ridge only 40 kilometers away in an air line.

For comparison I have five examples of nearly topotypical *bogotensis* which I took along the crest of the western Andes on the rim of the Dagua Valley. Also the specimens of *anchicayae* have been extensively compared with seedeaters in the collections of the United States National Museum and the American Museum of Natural History, including the type of *bogotensis*. Grateful acknowledgment is made of the courtesies extended by Herbert Friedmann and Dean Amadon who are in charge of these collections and to James Bond of the Academy of Natural Sciences of Philadelphia for the loan of examples of western Colombian seedeaters.

Museum of Vertebrate Zoology, Berkeley, California, November 30, 1959.

PHYSICAL ANALYSIS OF A SIMPLE BIRD SONG AS EXEMPLIFIED BY THE CHIPPING SPARROW

By PETER MARLER and DONALD ISAAC

The study of variation is an important means of obtaining indirect information about the effects of natural selection on the characteristics of animals. This paper is the first of a series of studies of variation in bird song, directed partly toward establishing adequate physical descriptions of bird vocalizations, and partly toward an attempt to infer from the nature and extent of variation something about the kind of selective influences to which song may be subjected (cf. Marler, *in press*). The methods are essentially those of the comparative anatomist applied in a new context. In discussing the effects of natural selection on the properties of bird song, we are embarking upon a subject which may be more akin to the study of cultural evolution in man than to organic evolution.

While morphological characters are under predominantly genetic control, we know that the species-specific songs of some birds are acquired during the life of the individual. Even where song traditions play no part in development, it is likely that genetic factors have only imprecise control over the detailed characteristics of the song (Marler, *in press*). However, in spite of the different mechanisms which ensure the perpetuation of the trait in the next generation, selection is likely to operate upon the final results in much the same way. Just as a genetic mutation which places its bearer at a disadvantage will be selected against, so any new learned tradition may be eliminated if it imposes some kind of biological disadvantage upon its users. In this way behavior may become as precisely adapted to its function as the structure of the body, even though it might be independent from detailed genetic control.

If we accept the position that the characteristics of bird songs are likely to be adaptive, we are then faced with the problem of explaining the remarkable degree of variation which they exhibit. Not only are there differences between geographically separated populations of the same species, but there are also marked variations between individuals in the same population, and even in successive songs of the same individual. Although most attention has been directed toward geographical variation, it is difficult to describe such variation adequately until we have a clear picture of the song repertoire of the individual.

As a first step, in a survey which we hope will ultimately throw some light on the significance of song variation, the Chipping Sparrow (*Spizella passerina*) has been selected as a simple case in which there is little audible variation in successive songs of an individual bird. The aim of this paper is to establish the limits of song variation in some individual Chipping Sparrows and to make some comparison between individuals, thus preparing the ground for treatment of other species in which singing behavior is more complex.

METHODS OF PHYSICAL ANALYSIS

The songs were all recorded in the field with a Magnemite 610–E tape recorder at a tape speed of 15 inches per second, using an Altec 633–A microphone mounted on an aluminum parabolic reflector. A Madison Fielding Micamp was used in the microphone circuit. The tapes were played back on a Viking Model 75 recorder adapted to operate at 15 inches per second. Analyses were made with a Kay Electric Company Sona-graph and Amplitude Display Unit, using the "high shape" filter setting in all cases.

Three types of analysis are presented in this paper. Most of the data come from the standard frequency/time analyses, using the wide band-pass setting. Since pitch is chiefly a function of frequency, these records can be read in much the same way as a musical score, from left to right. A small number of songs were analyzed for amplitude/time using the narrow band-pass setting and the ampli-

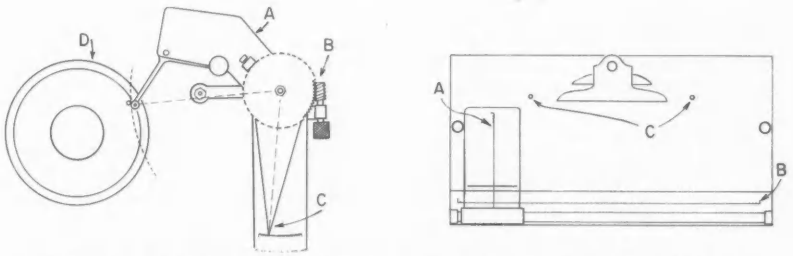

Fig. 1. Left, diagram of modification of sonagraph sectioning mechanism (top view). A, microswitch assembly for sectioner; B, worm and gear for controlling position of microswitch arm; C, pointer and calibrated scale; D, sonagraph drum with pin in place for tripping microswitch. The addition of the worm and gear, with its pointer and calibrated scale, allows precise control of the timing of tripping the sectioning microswitch in relation to the recorded signal.

Right, clip board for reading sonagrams. A sonagram sheet can be placed on this board and positioned so that its base line is matched to the horizontal mark on the sliding scale. A, transparent plastic slider with index lines and vertical scale calibrated for frequency to 50 cycles/second; B, horizontal scale calibrated for time to 5 milliseconds; C, positioning pins for sonagram sheets.

tude display unit. Single syllables selected from songs of several individuals were subjected to amplitude/frequency sectioning, with the narrow band-pass setting. The resulting sections are, in effect, histograms of the distribution of amplitude versus frequency at a selected point in the syllable. With the original sonagraph, sections can be made only at arbitrarily selected intervals of approximately 40 milliseconds (msec.). Since the syllables to be analyzed are also of about 40 msec. duration, no systematic information about their structure could be obtained. Therefore a worm gear and screw were added to the switch assembly of the sectioner (see fig. 1) which, coupled with a pointer and calibrated scale, made it possible to move the position of the switch arm in relation to the recording drum in scale increments as small as 2.5 msec.

Since the usefulness of data for analysis depends upon the accuracy of measurement, the following steps were taken. First, sonagrams were prepared of recordings made from a calibrated signal generator at 1 KC/sec. steps from 1 up to 8 KC/sec., with the narrow band-pass setting. Two scales were made. One, for frequency, was taken directly from the signal traces and subdivided to the nearest 50 cycles/sec. The other, for time, was made by taking the duration of the record to be 2.4 seconds and subdividing to the nearest 5 msec. These scales were then incorporated in a clip board (fig. 1) on which the sonagrams could be fastened, with the baseline adjusted to the index mark on the frequency scale. Thus readings could be made to the nearest 50 cycles/sec. and to the nearest 1–2 msec. The reliability of the readings was checked by repeated observations by a second observer.

The recordings were made at two locations in México during the summer of 1958. At Cuauhtemoc, near Chihuahua, two birds were recorded as follows: bird 1, June 21, 52 songs, June 22, 28 songs; bird 2, June 22, 27 songs. At El Salto, in Durango, six birds were recorded as follows: bird 1, June 29, 1 song; bird 2, June 30, 5 songs; bird 3, July 1, 2 songs; bird 4, July 1, 1 song; bird 5, July 2, 2 songs; bird 6, July 2, 2 songs.

GENERAL DESCRIPTION

The Chipping Sparrow song is normally "a simple trill or series of rapid notes, all on one pitch and delivered in a voice of dull, unmusical quality" (Saunders, A Guide to Bird Songs, 1935). The time/frequency analysis reveals repetitions of more or less identical syllables at approximately constant intervals (fig. 2). So far only one syllable type has been found in each individual. The syllable structure may, however, differ from one individual to another, even if the birds are neighbors (fig. 2). There is some variation in loudness of syllables. The song begins softly and quickly builds up to a maximum

which is maintained to the end. Figure 2 shows this typical pattern of loudness, or more strictly, of amplitude modulation. Amplitude variations in other parts of the song may result from such things as movements of the bird's head. The overall pattern is thus a very simple one, and the extent of individual variation is not too difficult to define.

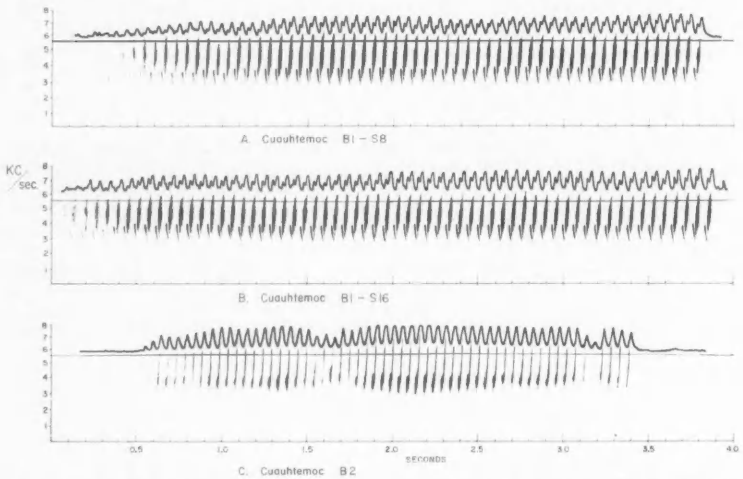

Fig. 2. Amplitude displays and frequency/time sonagrams of three songs selected from birds from Cuauhtemoc (A and B, bird no. 1; C, bird no. 2). The lower tracing in each record is the analysis of frequency/time and can be read from left to right in much the same way as a musical score. The upper record, in the form of a continuous line, registers the variation in loudness or, more strictly, in amplitude, of successive syllables of the song. The distance of the tracing above the base line is a function of the total amplitude at any one moment. Since it is only a relative measurement, we have arbitrarily referred it to the frequency scale on the left of the record.

ANALYSIS OF VARIATION

The songs of bird 1 from Cuauhtemoc.—Estimates of song variation in the individual are based on two continuous recordings of this bird made on consecutive days. No consistent differences were found between performance on the two days and the results are grouped together unless otherwise stated.

(a) Temporal pattern of singing. During sustained singing (fig. 3) the pause between songs (8.1±1.9 secs.) was more than twice the duration of the song (3.65±0.45 secs.). As expected, there is considerable variation in the interval between songs. The variation in song duration is more surprising, the longest songs being twice the duration of the shortest. Some other species such as the Brown Towhee (*Pipilo fuscus*) and the Oregon Junco (*Junco oreganus*) show less variation in this respect (Marler, MS).

(b) Number of syllables per song. The number of syllables per song is 55.1±6.7 (fig. 4). The distribution resembles that of song duration, and if we plot these against each other they fall into a linear relationship (fig. 4). The slope of the line corresponds with a rate of 15.1 syllables per second, irrespective of song duration.

(c) Frequency characteristics. Graphs of the maximum and minimum frequency from the sonagrams of each song reveal different degrees of variation (fig. 5). While the

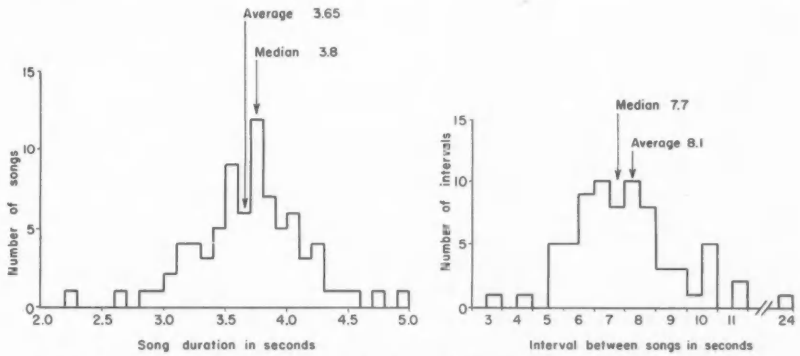

Fig. 3. Frequency distributions of song duration and intervals between songs for bird no. 1 from Cuauhtemoc. Song duration was measured from the sonagrams. The intervals between songs were measured with a stopwatch directly from the tape recording.

minimum is rather consistent, around 2.5 KC, the maximum, and therefore the frequency spread, have considerable variation. It is important to determine whether this frequency variation can be explained through varying rates of fading of the high frequencies with distance in comparison with the low frequencies, or whether it implies variations in actual production. A complete answer must await analysis of recordings

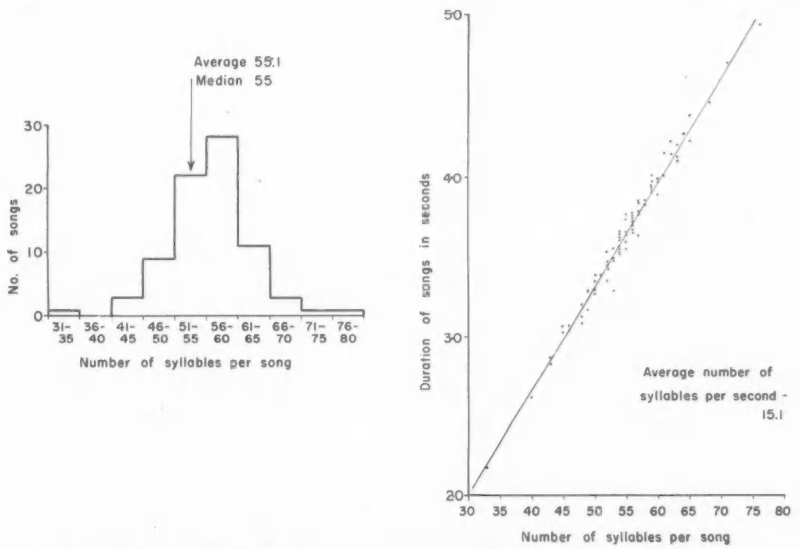
Average 55.1
Median 55
No. of songs
Number of syllables per song
Duration of songs in seconds
Average number of syllables per second - 15.1
Number of syllables per song

Fig. 4. Left, frequency distribution of number of syllables per song for bird no. 1 from Cuauhtemoc.

Right, plot of number of syllables per song against duration of song for bird no. 1 from Cuauhtemoc.

made under strictly controlled conditions. Meanwhile indirect evidence is available from a comparison of the frequency characteristics of different syllables in the same song and the pattern of amplitude modulation.

Eight songs from the first day were selected for amplitude analysis. The two presented in figure 6 are typical. The frequency range is narrow at the start of the song and broadens to a maximum which is more or less maintained to the end (A, B). The variation in maximum amplitude of the syllables follows a similar pattern (C). Thus the syllables with low maximum amplitude have a slightly higher minimum frequency (B) and a markedly lower maximum frequency (A). This is true of soft syllables, whether they are those with which a song always begins, or those sometimes occurring in other parts of the song (for example, song 1, syllables 10–20, song 2, syllables 30–50). It seems likely that much of the variation in frequency of songs recorded at a distance from the bird is a result of such amplitude variations, especially if allowance is made for the different attenuation rates of high and low frequencies with distance under different conditions (Pasquinelly, Ann. Epiphyties, 1954:49–62).

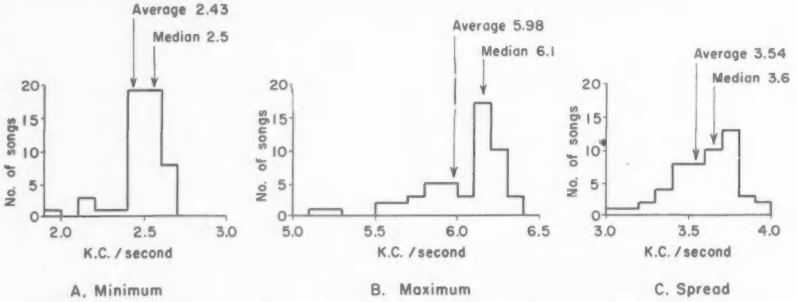

Fig. 5. Bird no. 1 from Cuauhtemoc (first day only): A, minimum frequency of song; B, maximum frequency of song; C, frequency spread of song. These measurements were made from wide-band sonagrams.

(d) Duration of syllables and syllable intervals. In addition to progressive changes in frequency and amplitude through the song there is also a measurable increase in the duration of syllables (fig. 6, D1 and D2) and a decrease in the intervals between syllables (fig. 6, E1 and E2) from the beginning to the end of the song. Once again allowance must be made for the effects of amplitude variation. A low relative amplitude is associated with a reduction in syllable duration and an increase in the interval. Perhaps one of these measures is simply a function of the other in which shorter notes result in longer intervals. If this were true, a graph of the sum of the two figures should form an approximately straight line, which is not the case (fig. 6, D1 and E1, D2 and E2). In fact in a sample of 31 songs of this bird, the interval between the start of successive syllables was found to be somewhat longer at the beginning and end of the song. This trend does not seem to be closely related to amplitude changes; but it is difficult to make measurements which are independent from amplitude effects to check this.

Two solutions to this problem were found. For some birds (see beyond) the loudest frequency in the syllable was selected, and the intervals between its onset in each syllable were measured through the song. For bird 1 from Cuauhtemoc the intervals between the inflections of frequency part way through the syllable could be measured (fig. 2) either directly, in syllables with high amplitude, or by extrapolation, in syllables

with low amplitude (fig. 6, F1 and F2). The changes in these measures through the song are broadly similar to those in the interval between the start of successive syllables, but there are longer intervals at the end of the song and shorter ones at the beginning. Again there is no discernible relationship with amplitude variations.

Thus there are at least two factors contributing to the detailed temporal pattern of the song as seen in a sonagram. A low relative amplitude at the start and in other parts of the song is associated with shorter syllables and longer intervals between syllables. This is superimposed on a basic tendency for more widely spaced syllables at the beginning and end of the song.

(e) Time, frequency and amplitude characteristics of the syllable. The normal frequency/time sonagram gives only an approximate picture of the structure of the syllable, even using narrow band-pass filters. More detailed analysis is possible by making amplitude/frequency sections, with the narrow band-pass setting, at short intervals through the syllable (see fig. 1). The duration of the syllables of bird no. 1 as determined

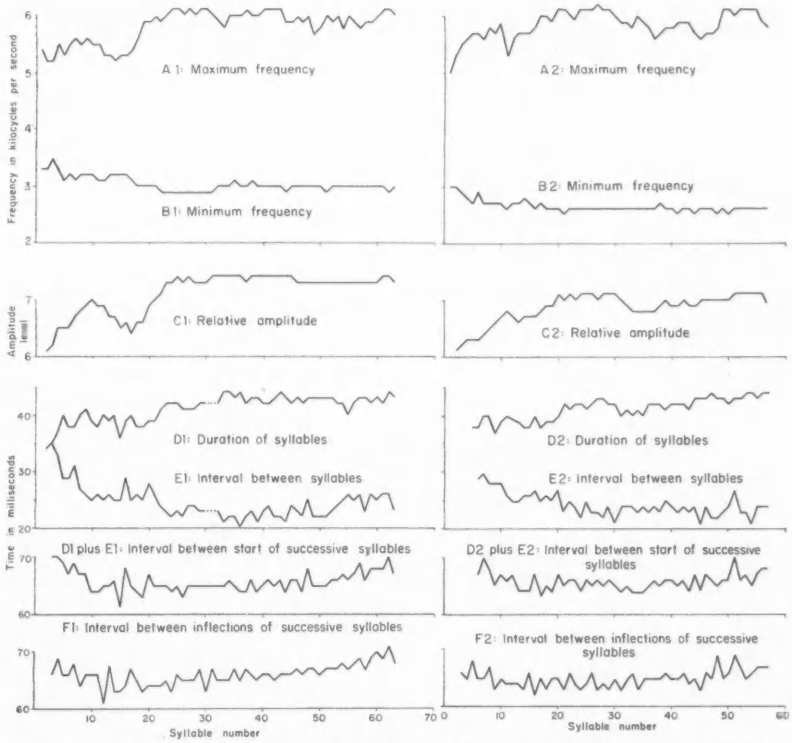
Frequency in kilocycles per second
A1: Maximum frequency
B1: Minimum frequency
A2: Maximum frequency
B2: Minimum frequency
Amplitude
C1: Relative amplitude
C2: Relative amplitude
Time in milliseconds
D1: Duration of syllables
E1: Interval between syllables
D2: Duration of syllables
E2: Interval between syllables
D1 plus E1: Interval between start of successive syllables
D2 plus E2: Interval between start of successive syllables
F1: Interval between inflections of successive syllables
F2: Interval between inflections of successive syllables
Syllable number
Syllable number

Fig. 6. Sequential analyses of two songs selected from bird no. 1 from Cuauhtemoc. The horizontal scale represents the sequence of occurrence of the syllables in the song (in certain cases the first one or two were too faint to make the particular measure and are not included). The amplitude graphs (C1 and C2) represent the maximum values for each syllable measured arbitrarily on the frequency scale (see fig. 2).

Table 1

Comparison of Song Measurements for Eight Chipping Sparrows from México[1]

		Cuauhtemoc		El Salto						
		Bird 1	Bird 2	Bird 1	Bird 2	Bird 3	Bird 4	Bird 5	Bird 6	Summary
A	Number of songs analyzed	80	27	1	5	2	1	2	2	.....
B	Average song duration in seconds	3.65±.45	3.08±.13	2.88	3.71	2.90	2.92	2.25	2.84	3.03 (2.25–3.71)
C	Number of syllables per song	55.1±6.7	55.1±2.5	54.0	63	48.5	56.0	46.5	54.0	54.0 (46.5–63.0)
D	Average syllables per second	15.1±0.2	17.9±0.3	18.8	17.0	16.7	19.2	20.7	19.0	18.1 (15.1–20.7)
E	Syllable duration in milliseconds	43.3±1.2	33.3±2.4	37	35.5	49.0	39	.....	36.5	39.1 (33.3–49.0)
F	Average minimum frequency in KC/sec.	2.43±.14	2.42±.10	3.2	2.9	2.4	2.9	.....	3.2	2.8 (2.4–3.2)
G	Average maximum frequency in KC/sec.	5.98±.27	6.52±.19	7.0	6.7	6.3	6.5	.....	6.2	6.5 (6.0–7.0)
H	Average frequency spread in KC/sec.	3.54±.20	4.10±.25	3.8	3.8	3.9	3.6	.....	3.0	3.7 (3.0–4.1)

[1] Note that the term average is used as a synonym for the arithmetic mean. While the table is self-explanatory, individual figures are subject to the following conditions: Bird 1, from Cuauhtemoc, B–G represent calculated averages and standard deviations (B–E for whole sample, F–H for first day only); bird 2, from Cuauhtemoc, B–H represent calculated averages and standard deviations for whole sample; birds 1 and 4, from El Salto, represent actual measurements from a single record each; birds 3, 5, and 6 represent average values for two records each (bird 5, E–H, record too poor for these measurements); bird 2, from El Salto, B–H represent average values of five recordings; summary, B–H represent averages and extremes of the average values given for all of the birds involved.

directly from the wide band, frequency/time analysis is about 43 milliseconds in the latter part of the song (fig. 6, D1, D2). Figure 7A presents a series of 18 sections at 2.5 millisecond intervals through such a typical, high amplitude syllable.

We see a different structure in the two parts of the syllable. The first downward-inflected note is a single tone, with the widest frequency spread in the middle. The peak frequency falls continuously with time and then levels out at about 3.5 KC. Then ampli-

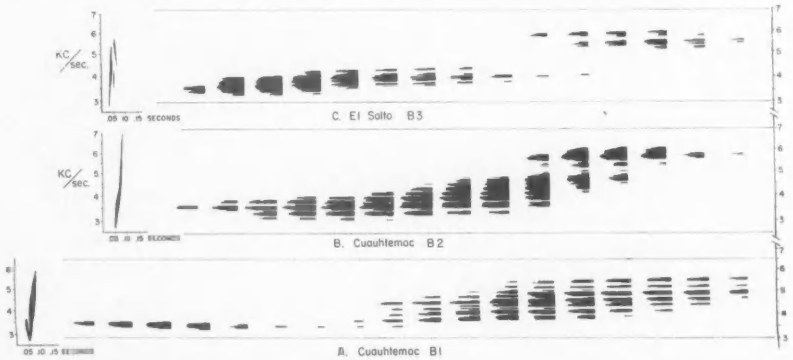

Fig. 7. Serial sections of syllables selected from songs of three different birds. A, bird no. 1 from Cuauhtemoc; B, bird no. 2 from Cuauhtemoc; C, bird no. 3 from El Salto. Wide-band frequency/time sonagrams of the syllables are shown at left. Amplitude/frequency serial sections are illustrated at right, proceeding from left to right through the syllable at 2.5 millisecond intervals.

tude declines, but before this note dies out it is joined by first one and then several overtones at about 250 cycle intervals. From this point onward each note and its overtones tend to rise in frequency. But the overall change in frequency characteristics is achieved by a transfer of emphasis from lower to higher overtones, the lower ones fading and dropping out and additional higher ones coming in.

By this method we can thus obtain a rather complete picture of the frequency structure of the syllable and the comparison with songs of other individuals which follows is largely concerned with these details of syllable structure.

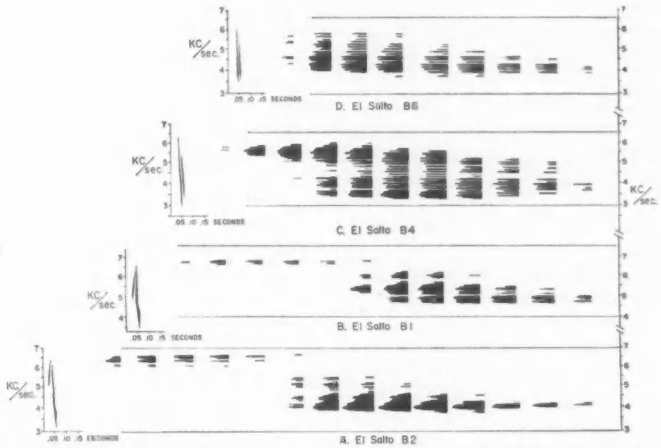

Fig. 8. Serial sections of syllables selected from songs of four birds from El Salto: A, bird no. 2; B, bird no. 1; C, bird no. 4; D, bird no. 6. Wide-band frequency/time sonagrams of syllables are shown at left. Amplitude/frequency serial sections are illustrated at right, proceeding from left to right through the syllable at 2.5 millisecond intervals.

A comparison of the songs of eight Chipping Sparrows.—In addition to the extensive recordings of bird 1 from Cuauhtemoc, brief recordings were also made of one bird adjacent to bird 1, and of six birds in an area 400 miles to the south at El Salto (see page 125). Usually only one or two songs were recorded, which limits this analysis to certain aspects of variation, particularly that involving syllable structure. Before considering this, the other characteristics will be reviewed briefly. For purposes of comparing variability, standard deviations are given for measures of the two larger samples from the birds from Cuauhtemoc (table 1).

General characteristics. Average song duration (3.03 seconds for the whole sample) varies somewhat between individuals but in most cases falls within twice the standard deviation of the average for Cuauhtemoc B1. In contrast with this, the number of syllables per second is more or less constant within the individual, and the differences found between individuals are probably consistent. In spite of these variations the sample as a whole fell within quite narrow limits with an average of 18.1 syllables per second and extreme values of the averages for each individual of 15.1 and 20.7. Last of the temporal characteristics to be measured is syllable duration, which is subject to change with loudness, as described previously, and thus varies considerably within the individual.

The differences between individuals recorded here are probably not reliable, although it is likely that if the comparison had been restricted to high amplitude records, consistent inter-individual differences would have been found.

A sample of songs from all birds was measured for spacing of syllables through the song. Intervals between either an inflection in the syllable, or between the onset of the dominant frequency, were measured in the first ten and the last ten syllables and compared with a sample of ten from the middle of the song. In every case the average interval in the middle of the song was shorter than that at the beginning and end, indicating the same trend as in bird 1 from Cuauhtemoc.

Frequency characteristics are also subject to variation with amplitude, especially in the upper part of the scale. Thus the maximum frequency varies more in the individual than the minimum frequency. Whereas individual differences in maximum frequency are not consistent, those in minimum frequency may be significant. The average spread of frequency is fairly consistent through the whole sample.

Syllable structure. As can be seen from the frequency/time analyses (figs. 2, 7, and 8), syllable structure is similar in some individuals and different in others.

The variations in syllable structure are seen more clearly in the serial sections. The three birds illustrated in figure 7 show marked differences in detailed structure. In comparison with bird 1 from Cuauhtemoc (A), which has already been described, bird 2 from Cuauhtemoc (B) lacks the initial note with a downward inflection and has a discontinuity in the rising note which, incidentally, is not evident on the frequency/time analysis. These two birds had adjacent territories and were within earshot of each other. The third record (C) of a bird from El Salto shows another syllable type with first a rising and then a falling inflection. In contrast, figure 8 shows two pairs of songs with very similar syllable structure, all drawn from the same population.

In spite of these variations in syllable structure, we notice that all birds share the characteristic pattern of overtones, with changes in overall frequency resulting largely from a shift in emphasis from one overtone to another. The tonal quality of the notes which make up the syllable must be strongly affected by this overtone structure. Comparative studies of such serial sections will provide the best means of discovering whether there are any species-specific tonal qualities in bird song which might be used in species recognition. The overtone pattern also has implications for the mechanism of sound production, the shift of emphasis being perhaps more likely to result from changes in the dimensions of resonating cavities than from changes in the mechanism producing the fundamental frequencies.

DISCUSSION

The temporal pattern of singing.—The Chipping Sparrow was chosen for this study because its song is simple and "monotonous," varying relatively little within the individual. In particular, we do not find individuals with a multiplicity of song themes, such as many more "versatile" song birds employ. Hartshorne (Auk, 73, 1956:176–192) has pointed out a general relationship between the variability of a species' song and the time it spends in song. The more versatile species tend to be "continuous" singers, and the more "monotonous" or "non-versatile" ones to be discontinuous singers. Discontinuous singers are broadly defined as those which are actually singing for less than 30 per cent of the performance time. Bird 1 from Cuauhtemoc, an example of a highly non-versatile singer, sang for 31 per cent of the performance time, which is a good approximation to Hartshorne's estimate. At least in these records, made in the midmorning, the Chipping Sparrow is no exception to the generalization, although Saunders (*op. cit.*) points out it may sing more continuously just after dawn.

In some species the hypothesis is more difficult to apply. In certain cases this is a result of our ignorance of the extent of "versatility," a property of which our ears may be a poor judge. Thus in the European Willow Warbler (*Phylloscopus trochilus*) which Hartshorne cites as an extremely non-versatile singer, the individual may actually have a number of themes. A series of 47 consecutive songs was recorded near Cambridge, England, on May 15, 1957. The sonagrams have not yet been analysed in detail, but there are at least a dozen different themes and the basic themes are also modified in many different ways in consecutive songs. Conversely one can be overimpressed by the variation of some of the versatile singers by just listening to them. There is sometimes a great deal of repetition of themes by the Song Thrush (*Turdus ericetorum*), which is regarded as a highly versatile singer. We need more quantitative information on individual variation before Hartshorne's interesting generalizations can be tested.

A second problem arises in determining the degree of continuity of the singing of birds like thrashers and mockingbirds. The briefness of the pauses occurring at very frequent intervals may give an impression of continuity in birds which are actually silent for a relatively high proportion of the performance time. It is necessary first to ascertain what actually constitutes a single song in a versatile singer before the temporal characteristics of the singing can be worked out.

Song as a means of specific and individual recognition.—The question of which properties of a song may be used in specific and individual recognition can only be finally answered by experiment. However, indirect evidence may be obtainable by the study of natural variation. In general we may expect that characteristics functioning as means of recognition, if they exist, will appear consistently in the songs of the individual. Those which could be used for individual recognition should differ from bird to bird, while those for species recognition should be consistent in all members of the species, or at least in all members of a population.

For specific recognition it is a prerequisite that the song should be readily distinguished from those of other species likely to be heard at the same time and place. Comparative study is therefore necessary to determine which characteristics of the song may be important, and we do not yet have the necessary information to make this possible in the Chipping Sparrow. However, we can speculate about the properties which could be used in individual recognition.

General frequency characteristics are unlikely to be useful for individual recognition in the Chipping Sparrow, since they vary with the loudness of the song and attenuate differently with distance. Song duration and the number and duration of the syllables also vary widely within the individual. Most consistent within the individual are (a) the rate of syllables per second and (b) the detailed frequency/amplitude structure of the syllable. However, pairs of birds have been found within the population at El Salto whose songs are very similar in one or both of these characteristics. In these cases it is difficult to see how reliable individual recognition would be possible. The detailed resemblance between songs of some members of the same population seems to imply a degree of causal relationship, but only further experimentation can tell whether this is a result of genetic factors, of learning, or simply of chance.

Serial frequency/amplitude sectioning as a method of song analysis.—It has been suggested that the distinctive tonal quality of the songs of some birds may be important in specific recognition (Thorpe, Ibis, 100, 1958:535–570). The physical properties which convey this tonal quality, including in particular the patterns of overtones, are difficult to discern from the wide band, frequency/time sonagrams most commonly used. We believe that the method of frequency/amplitude serial sectioning described in this paper can give valuable information about these details of note structure.

For example, although individual differences in syllable structure are evident in the Chipping Sparrow, birds from both populations share the same overtone structure. The intervals between overtones vary. Those in bird 1 from Cuauhtemoc are about 250 cycles apart, and in bird 2, where they are less regular, about 200 cycles apart. In birds 1 and 2 from El Salto they are irregular, but in birds 4 and 6, there is a remarkably regular pattern of as many as 18 simultaneous overtones at 100 cycle intervals. It is conceivable that this pattern of several, evenly spaced overtones is distinctive of the song of the Chipping Sparrow and might be used in specific recognition.

The problem of making reliable measurements from sonagrams.—Some of the data presented in this paper are derived from fine measurements, which are susceptible to sources of error from which coarser measurements are free. In the first place we must not forget that a natural sound is subject to many distortions before a sonagram is obtained. Frequency response in particular is influenced by the characteristics of microphone, recorder and playback amplifiers, the setting of the "shaping" switch on the sonagraph, and the band-pass settings which are used. The final measurements are relative and it is therefore necessary to state the conditions under which they are made.

For example, the frequency measures given in this paper are taken from sonagrams made with the wide-band setting, which distorts by expanding the apparent frequency spread of a given note. The reason for using this, rather than the narrow-band setting, is that wide band sonagrams reveal the temporal characteristics of the sound most clearly. While the measures of frequency are thus distorted, the distortion is a systematic one, so that the results can be used for comparative purposes. However, if comparisons are to be made between sonagrams from different machines it is necessary to calibrate each sonagraph.

In addition to these instrumental effects, attention has been drawn to the more subtle influence which variations in amplitude can have, both on the temporal and on the frequency characteristics of a sound. Especially when fine measurements are being made, such variations must be taken into account if the results are to be meaningful.

SUMMARY

As the first subject in a series of studies of variation in bird song, the Chipping Sparrow was selected because of the relatively slight degree of variation within the individual. The extent of this variation is traced in a large sample of songs of one bird (bird 1) and comparisons are then made with smaller samples from seven individuals. All recordings were made at two locations in México, in Chihuahua and in Durango.

In bird 1, the average values for 80 songs are: song duration, 3.65±0.45 seconds; interval between songs, 8.1±1.9 seconds; number of syllables per song, 55.1±6.7; rate of syllables per second, 15.1±0.2; minimum sound frequency, 2.43±0.14 KC/sec.; maximum frequency, 5.98±0.27 KC/sec.; frequency spread, 3.54±0.20 KC/sec. The interval between the start of successive syllables is longest at the beginning and end of the song. Superimposed on this is an apparent reduction in syllable length where the amplitude is relatively low. This amplitude variation also has an effect on frequency characteristics and must be taken into account in making precise measurements.

A new device is described for modifying the sonagraph to make frequency/amplitude sections serially through a syllable at intervals down to 2.5 milliseconds. Analysis of syllable structure by this means reveals, in bird 1, an elaborate pattern of evenly spaced overtones, with the overall changes of frequency effected mainly by a shift of emphasis from one overtone to another.

A comparison with the songs of the seven other birds reveals differences in syllable structure, which are sometimes striking, even between neighboring birds. However,

some adjacent birds had a very similar syllable structure. All songs analyzed showed signs of the same pattern of multiple, evenly spaced overtones. Significant individual differences, which might be used in individual recognition, were found in the number of syllables per second, and possibly in syllable duration and minimum frequency in some cases. Differences in other frequency characteristics, song duration and number of syllables per song are probably not statistically significant as determined from these samples.

ACKNOWLEDGMENTS

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Department of Zoology, University of California, Berkeley, California, August 5, 1959.

FROM FIELD AND STUDY

Changed Status of Several Species of Waterfowl in Alaska.—Waterfowl technicians have long recognized that during periods of severe drought in the Canadian prairie provinces ducks move farther north to seek a favorable environment. How far beyond their normal range various species will travel and how successfully they might produce young under displaced circumstances has been a matter of conjecture. In the summers of 1957, 1958, and 1959 biologists studying waterfowl production made several observations bearing on this question near Tetlin, Alaska (63° N, 142° 30′ W), and on the Copper River Delta (60° 30′ N, 145° 30′ W).

Anas discors. Blue-winged Teal. This teal has been reported infrequently since the earliest days of ornithological work in Alaska, but a specimen had not been collected and preserved to verify the reports until September 4, 1952. On that date James W. Brooks collected two near Fairbanks, one of which was an immature female. Since then they have been checked in hunters' bags and reported occasionally by other observers from widely scattered points in Alaska. Only one breeding record had been established to date, however. Bob L. Burkholder observed an adult with two ducklings on July 13, 1949, near Palmer in the Matanuska Valley (Kessel, Condor, 57, 1955:372–373).

A banding station has been operative in the Tetlin area since 1955 and an intensive production study since 1957. Blue-winged Teal were not reported there until 1958 when six were sighted. In 1959 they were common. Sixteen broods were observed of which a complete count was obtained on 12 for an average brood size of 7.2. This compares favorably with brood size of Blue-winged Teal within their optimum range. In addition to 25 banded and released, two adult and one flightless young were collected for specimens and deposited in the University of Alaska Museum and the United States National Museum, Washington, D.C. Blue-winged Teal were observed and checked frequently in hunters' bags in September of 1959 as far west in Alaska as the Fairbanks area and along the coast of southeastern Alaska. These cumulative observations would indicate that, in some years at least, the Blue-winged Teal is a rather common summer resident locally.

Aythya americana. Redhead. Gabrielson and Lincoln (Birds of Alaska, 1959:177) state that "The inclusion of the Redhead in the avifauna of Alaska is upon limited evidence." The few reports are from sight records at Kodiak and in the Aleutian Islands. The most recent report was by Murie in 1936 from Amukta Island in the Aleutians.

On May 23, 1959, John Hakala observed a pair of Redheads on the Kenai National Moose Range. During the week prior to May 20, 1959, Peter Shepherd and Charles Trainer, working on the Copper River Delta near Cordova, observed a pair of Redheads on several occasions in company with a male Canvasback. From the middle of June through the summer, Redheads were observed regularly in the Tetlin area. Of 71 trapped, two were flightless young from different broods. Another brood of three was sighted but not caught. Seven Redheads, including the two young, were saved for study skins and deposited with the University of Alaska and the National Museum. Sixty-four were banded and released. Among those trapped on August 1, 1959, was a female which had been banded as an adult near Ardmore, Oklahoma, on March 30, 1953.

Aythya collaris. Ring-necked Duck. With but one exception the few records of the Ring-necked Duck have come from on or near the coastal islands of Alaska, from southeastern areas to the Aleutians. The exception was a specimen taken near Fairbanks on August 7, 1953.

Adult Ring-necks have been sighted in limited numbers each summer since 1957 in the Tetlin area and a few have been trapped and banded. An adult male was collected for the University of Alaska Museum in August of 1958 and another adult male on August 29, 1959. On September 5, 1958, near Napakiak, Alaska, on the lower Kuskokwim River a banded duck mistakenly reported as a Lesser Scaup was taken in a fish net. This duck had been banded as an adult male Ring-neck near Akron, Ohio, on April 4, 1957. This, then, definitely extends the distribution of the Ring-necked Duck across interior Alaska from the Bering Sea to the Canadian border, although nowhere within this range has it yet been identified as a breeding species.

Aythya valisineria. Canvasback. Gabrielson and Lincoln (*op. cit.*:180) state that "The Canvasback is uncommon in Alaska, and the only unquestioned breeding records are from the Yukon Valley," following which, they list several sight records of both adults and broods at widely scattered points in Alaska.

Since 1955 Canvasbacks have been recorded regularly on the aerial breeding population survey

in east-central Alaska; that is, at Ft. Yukon Flats, Minto Lakes, and Tetlin. In recent years they have become quite abundant in this restricted range and have spread over a much larger area than formerly. In 1959 Canvasbacks were seen frequently from the lower Kuskokwim River up the Bering Sea coast north to Kotzebue Sound and all across interior Alaska to the Canadian border. Of nine nests under observation on the Copper River Delta, seven hatched with an average brood size of 5.8 young. Canvasbacks were more abundant in the Tetlin area than in any previous year. Two flocks of more than 1500 each were observed there on Butterfly and Old Albert lakes, from which 309 were banded. These were largely flightless adult males, but in addition 32 broods were tabulated. These observations of recent years indicate that the Canvasback is a common summer resident in much of Alaska and is abundant in some areas.

Oxyura jamaicensis. Ruddy Duck. The only previous record for the Ruddy Duck in Alaska was on August 15, 1916, at Totem Bay near Petersburg when two were seen and a male was collected (Gabrielson and Lincoln, *op. cit.*:239).

On June 1, 1957, Dan Rose took a Kodachrome picture of a pair of Ruddies near the airstrip at Northway, Alaska, about 25 miles east of Tetlin. On several occasions in the summer of 1959 a few Ruddy Ducks were observed near Tetlin. On August 19 an adult female was taken in the banding trap and saved for a study skin. On August 25 in a different lake system a female and brood of five downy young were observed. One of the young, a male, was collected the following day and subsequently sent to the United States National Museum with the adult female collected earlier. This constitutes the farthest northwest record for the Ruddy and the first breeding record for Alaska.

A drought in the north-central United States and the prairie provinces of Canada became very acute in 1959. As shown by the aerial breeding population surveys, species of waterfowl that are primarily prairie nesting were much more abundant generally in Alaska and the Northwest Territories than in the previous ten years. The present drought, however, is the most severe and extensive of any experienced since aerial surveys have been made in the far north. It is reasonable to assume, then, that the occurrence of these species in Alaska in 1959 is not necessarily unique. Undoubtedly in former droughts of equal or greater severity the range of several species was extended this far but nobody was on hand to record the phenomenon. Or perhaps some of the early, doubted records were made during years of climatic conditions in the south paralleling those of 1959 and absence in the interval between has led to discrediting of the earlier observations.

The most significant and intriguing feature of this "extension of range" is the fact that the stable Arctic and sub-Arctic regions may be an effective reservoir for displaced waterfowl during adverse times in their normal range.—Henry A. Hansen, *Bureau of Sport Fisheries and Wildlife, Juneau, Alaska, October 30, 1959.*

Behavioral and Ecologic Notes on the Brown-headed Cowbird.—On August 14, 1958, on the campus of the University of California, Berkeley, California, I watched for one-half hour an adult female Oregon Junco (*Junco oreganus*) repeatedly feed an almost fully-grown, juvenal-plumaged Brown-headed Cowbird (*Molothrus ater*). The young cowbird persistently postured in food-begging display: wings raised and fluttering, bill agape, with a continual *zweet*! note given at a rate of six or seven each five seconds. It is likely this young cowbird was one actually reared by the junco, not merely one that had "adopted" the junco after having been fledged; the support for this inference lies in the length of time the bond persisted between the two birds, in spite of some insistent disturbance of the birds on my part. Friedmann (The Cowbirds, 1929:279) remarked that the bond between a fledged juvenal cowbird and a temporarily adopted foster parent is exceedingly loose.

This particular juvenile was of interest in that it uttered notes of alarm or anxiety, a phenomenon unknown to Friedmann (1929:273) but apparently of some frequency in cowbirds in Texas (Robert K. Selander, personal communication). Whenever I approached the birds, which were mostly active on the ground, they flushed into nearby small trees; the cowbird always flushed first and gave sharp, clear alarm notes of high frequency: *pip-pip-pip*. The notes had the quality and phrasing of many emberizine alarm notes and were unlike any notes from cowbirds I have otherwise heard or found described. This is not to imply the cowbird mimicked the notes of the junco, for the alarm notes of the attendant junco were of higher frequency and of different phrasing, as: *titit, titit*.

In passing it may be noted that the Oregon Juncos of west-central California (*J. o. pinosus*) seem not heretofore to have been recorded as hosts of Brown-headed Cowbirds (Friedmann, 1929; Auk, 48,

1931:52–56; Condor, 35, 1933:189–191; Wilson Bull., 46, 1934:25–36; Auk, 60, 1943:350–356; Auk, 66, 1949:154–163).

Friedmann (1943:356) listed Song Sparrows of the race *Melospiza melodia samuelis* as hosts of this cowbird; this was based on a record at Soap Lake, Gilroy, Santa Clara County, California. The nomenclature is in accord with that of the fourth edition of the A.O.U. Check-list of North American Birds (1931), and thus refers to Song Sparrows now called *M. m. gouldii* in the fifth edition of the Check-list (1957). Additionally, Friedmann had earlier (1934:114) listed *M. m. santaecrucis* as a host, on a record made at Irvington, Alameda County, California; the nomenclature here is apparently that of Grinnell (Pac. Coast Avif., 18, 1927:119), and it also refers to Song Sparrows today called *M. m. gouldii*.

This confusion in nomenclature is of no significance in itself, but it renders obscure the relationship of cowbirds to hosts within a vegetation type to which Brown-headed Cowbirds are seemingly little attracted, that of the Pacific coastal salt-water marshes. Two instances of parasitism by cowbirds validly pertaining to *M. m. samuelis* as the host in a true salt marsh have already been published (Johnston, Condor, 58, 1956:29) but the significance of these records was not appreciated at the time. These two instances are the second and third known layings of cowbirds within the vegetation of salt marshes (see Friedmann, 1949:16). On San Francisco Bay marshes Song Sparrows place their nests within clumps of pickleweed (*Salicornia ambigua*), cordgrass (*Spartina foliosa*), or gumplant (*Grindelia cuneifolia*). The nests of the Song Sparrows parasitized by Brown-headed Cowbirds were placed in gumplant shrubs, that is, in that vegetation most closely resembling the life form of some plants found within "normal" habitats of cowbirds. One egg of a cowbird was in each nest, the first of which was found on May 12, 1955, ten inches above ground level, containing two eggs of the host; the second nest was found on June 6, 1955, nine inches high, and contained three eggs of the host. The first clutch was deserted and the second, judged later from the beaten and plate-like appearance of the nest, hatched and fledged at least the cowbird.—Richard F. Johnston, *Museum of Natural History, University of Kansas, Lawrence, October 2, 1959.*

Occurrence of the Osprey in Uruguay.—Recently on two occasions I have observed the Osprey (*Pandion haliaetus*) in Uruguay, thus extending the known range of this hawk south to this country and to latitude 35° south on the Atlantic Coast of South America. Heretofore migratory Ospreys have been recorded south to latitude 42° in Chile, to Tucumán in Argentina, to Lambaré in Paraguay, and to Torres at 29° in Brazil (Hellmayr and Conover (Cat. Birds Amer., pt. 1, no. 4, 1949:234–236).

On February 11, 1959, my wife and I were camping at Playa Penino, 30 kilometers west of Montevideo on the Río de la Plata. At this locality the salinity is low and fish are plentiful. Here an Osprey arose among a group of aquatic birds and was observed carefully for several minutes. On February 22 at the same place, an Osprey was again seen and watched as it caught a fish. The bird was in sight for an hour.—Rodolfo Escalante, *Montevideo, Uruguay, October 22, 1959.*

Another Record of the Baikal Teal in Northwestern Alaska.—A pair of Baikal Teal (*Anas formosa*) was observed on May 28, 1959, at Cape Sabine, Alaska. The birds were flushed from a small tributary of the Pitmegea River at a point two miles from the Arctic Ocean. They flew across the river and landed on a gravel bar fifty yards away where they preened for several minutes before flying up the river. Conditions for observation were very good; it was a clear evening and the sun was at my back. I did not recognize the birds in the field, but instead made a detailed sketch of the male, which was later readily identifiable. The male was in breeding plumage. The markings of the male are so bizarre that there is no likelihood of misidentification. I was in the field at this locality from May 20 to 29, and from June 12 through August 11. The teal were not seen again.

This species was first recorded in North America by A. M. Bailey who collected a male on September 21, 1921, at Wainwright, Alaska (Condor, 26, 1924:195). Five records have been published subsequently. Two males were taken on King Island on May 23 and 25, 1931 (Bailey, Auk, 50, 1933: 97). Collins collected a pair in breeding plumage on St. Lawrence Island on July 23, 1937 (Gabrielson, Auk, 58, 1941:400). A second pair in breeding plumage was taken at Wales on June 8, 1942, and a male was collected, also at Wales, on June 22, 1944 (Bailey, Colorado Mus. Nat. Hist., Popular Series,

No. 8, 1948:165). Although only two of these records are of pairs taken in the breeding season, it has been presumed that the species probably bred in small numbers in western Alaska. It is reported that the first nesting record for Alaska has been obtained by Don Bleitz in June, 1959, at Hooper Bay (News from the Bird Banders, 34(3), 1959:40). No details of the nesting are given.

The occurrence of a mated pair of Baikal Teal in late May at Cape Sabine, coincident with the onset of breeding in the local population of Pintails, strongly suggests that the species nests occasionally in northwestern Alaska. This locality is 200 miles north of previously recorded pairs.

This observation was made while the writer was engaged in a project supported by the Arctic Institute of North America under contract with the Office of Naval Research.—WILLIAM J. MAHER, *Museum of Vertebrate Zoology, University of California, Berkeley, California, September 22, 1959.*

Occurrence of Slaty and Dwarf Vireos in Jalisco, México.—In the course of field work in the Sierra de Autlán, 12 miles south of Autlán, southwestern Jalisco, México, in April of 1959, one of my Mexican assistants, Nazario Chávez, had the good fortune to collect specimens of both the Slaty Vireo (*Neochloe brevipennis*) and the Dwarf Vireo (*Vireo nanus*). These represent considerable extensions of the known ranges of these species.

According to the Mexican Check-list (1957), *Neochloe brevipennis* was known previously from Oaxaca, Veracruz, and Guerrero [also occurs in Morelos, see p. 88 of this issue.—editor]. *Vireo nanus* was previously known from Oaxaca, Guanajuato (5 mi. NE Irapuato), and Michoacán.

Our camp, in the Sierra de Autlán, was at an estimated elevation of 8000 feet in humid pine-oak forest. The vegetation zone name used here follows Leopold (Ecol., 31, 1950:507–518), but the zone itself, in the Sierra de Autlán, is not typical of Leopold's pine-oak forest. The oaks at this locality were very tall (60 to 90 feet) and were festooned with mosses, liverworts, and other epiphytes. There was a dense understory of rank herbaceous plants. Both of these vireos were called in to the vicinity of the collector by use of a combination of "squeaking" and "pigmy owling," using in the latter case the bell-like notes of *Glaucidium gnoma*, which is also present in this range.

Other species of interest, found in association with the two vireos at this locality, included the Chestnut-sided Shrike-vireo (*Vireolanius melitophrys*), the Scaled Antpitta (*Grallaria guatimalensis*), the Olivaceous Woodcreeper (*Sittasomus griseicapillus*), the Aztec Thrush (*Ridgwayia pinicola*), and the Cazique Hummingbird (*Lampornis amethystinus*), and a single Flammulated Owl (*Otus flammeolus*) which was caught in a nylon "mist" net placed across a small, heavily wooded arroyo. This last specimen also represents an extension of the known range of this species.

Grateful acknowledgment is made to the Western Foundation of Vertebrate Zoology at Los Angeles, for financial aid to complete my field studies, and also for much moral support and encouragement. All specimens mentioned above are deposited in the collections of the Foundation.

The specimen of the Slaty Vireo has been compared with the type of *Neochloe brevipennis browni* at the Museum of Vertebrate Zoology and proves to be referable to the nominate race *N. b. brevipennis*.—W. J. SCHALDACH, JR., *Colima, México, September 22, 1959.*

Rare Migrants in Death Valley National Monument, California.—On the morning of May 10, 1959, a single Northern Waterthrush (*Seiurus noveboracensis*) was observed in good light for several minutes at Wildrose Campground, elevation 4000 feet, in the Panamint Mountains, Inyo County, California. The bird was walking along a small ditch and seemed unafraid at my close approach. This species is not listed by Grinnell and Miller(Pac. Coast Avif. No. 27, 1944:409) as recorded east of the Sierra Nevada in California. Linsdale does not include the species in his list of the birds of Nevada (Condor, 53, 1951:228–249).

A single male Bobolink (*Dolichonyx oryzivorus*) was seen at Cow Creek, in Death Valley National Monument on May 25, 1959. It was perched on a tamarisk tree for several minutes which afforded me a very good observation before it flew up canyon toward the Funeral Mountains. The species was recorded in Mono County in 1901 (Fisher, Condor, 4, 1902:11). This is the nearest record in the state. Linsdale lists the species as "transient" in Nevada, and one of the two existing Nevada records occurred in the Toyabe Mountains, Nye County, east of Death Valley.—ROLAND H. WAUER, *Death Valley National Monument, Death Valley, California, August 5, 1959.*

Breeding of the Fork-tailed Petrel off the Washington Coast.—The fifth edition of the A.O.U. Check-list of North American Birds (1957) and Bent (U. S. Nat. Mus. Bull. 121, 1922:137), list the Fork-tailed Petrel (*Oceanodroma furcata*) as breeding on islands off the coast of Washington. However, Jewett, Taylor, Shaw, and Aldrich (Birds of Washington State, 1953:74), and Dr. Alexander Wetmore in a personal communication, agree that this statement is based on a questionable egg record and that there is no authentic breeding record of this petrel for Washington, although there are good breeding records for sections of the coast to the north and the south. Consequently, it seems worth recording that on July 17, 1959, Garrett Eddy, William Hawkins, Karl Kenyon, and I discovered numerous burrows of Fork-tailed Petrels containing adults, young, and eggs, on Bodelteh Islands off Cape Alava, Clallam County, Washington.

The two main Bodelteh Islands, of approximately five and ten acres each, lie about a mile offshore and are part of the Flattery Rocks group. They have steep, rocky slopes, generally brush-covered and leading to somewhat level, wooded top areas over 190 feet high. The burrows of the petrels were usually two to four feet deep on steep, rocky, sparsely vegetated areas from 20 feet or so above high tide to over 150 feet. Typically they started in crevices or under rocks and continued, with some excavation of soft earth, to the nesting chamber. After finding the first two petrels, one on an egg and one on a newly hatched young, Eddy and I found some seven more occupied burrows in perhaps one hour's additional search. Six of these held single young, up to about two weeks old, but no adults. Judging from our observations and those of Kenyon and Hawkins, the population of breeding Fork-tailed Petrels on Bodelteh Islands must consist of many hundreds of pairs.

Burrow-nesting species associated with the Fork-tailed Petrels on Bodelteh Islands were Leach Petrels (*Oceanodroma leucorhoa*) and Cassin Auklets (*Ptychoramphus aleutica*). Hawkins found four Leach Petrels on eggs in burrows on the brush and grass-covered south slope of the eastern island. The several occupied auklet burrows were all situated on fairly open areas beneath trees on the flattish tops of the islands above the slopes where the petrels were nesting. They held young, one of which was nearly fledged.

Evidence was seen of considerable predation, presumably by some mammal. Eight sets of wings and partial pectoral girdles of Fork-tailed Petrels were found under bushes in the course of a limited search. The difficulty of landing on Bodelteh makes it seem unlikely that predators such as domestic rats have been introduced to the islands, so it is hoped a native predator is involved and something of a balance has already been reached between it and the population of the Fork-tailed Petrel.—FRANK RICHARDSON, *Department of Zoology* and *Washington State Museum, University of Washington, Seattle, September 29, 1959.*

An Occurrence of the Rose-breasted Grosbeak in Southern Nevada.—On May 17, 1959, a male and female Rose-breasted Grosbeak (*Pheucticus ludovicianus*) were seen by me at Indian Springs Ranch, Clark County, Nevada. The birds frequented the shrubby vegetation adjacent to the spillway of the larger of two small irrigation reservoirs on the ranch property. The vegetation here consists primarily of mesquite (*Prosopis juliflora*), four-winged saltbush (*Atriplex canescens*), and a tangle of cultivated blackberry (*Rubus* sp.). The birds remained in the area for several days. However, on May 24, the last date of observation, only the female was seen.

As far as is known the only previously reported occurrence of the Rose-breasted Grosbeak in Nevada is that of a single male bird observed over twenty years ago by Grater (Auk, 56, 1939:191) in the vicinity of Saint Thomas on the north arm of Lake Mead.—W. H. RICKARD, *New Mexico Highlands University, Las Vegas, New Mexico, October 27, 1959.*

The Rusty Blackbird and Dickcissel in Oregon.—On March 20, 1959, while watching a mixed group of Redwinged and Brewer blackbirds at the feeding station outside our window at Tillamook, Oregon, my wife remarked that there was an odd looking blackbird among them. It was collected to confirm my identification of it as a male Rusty Blackbird (*Euphagus carolinus*), a species hitherto unrecorded from Oregon. The specimen is now number 12420 in my collection.

On March 24, 1959, Mr. Paul Lewis told me of a bird that for several days had been visiting the feeding station at his home in Tillamook. He believed it to be a Dickcissel and asked me to check his identification. The following day I took several Dickcissel skins from my collection to the Lewis residence where, for more than 15 minutes, we watched the bird feeding just outside the window. I did

not hesitate to verify his identification of the bird as a Dickcissel (*Spiza americana*). Unfortunately, Mrs. Lewis did not wish the bird collected, so it can be reported only as a sight record. I was later advised that the bird remained around the feeding station two or three days longer and then disappeared. I know of no other record of the occurrence of this species in Oregon.—ALEX. WALKER, *Tillamook County Pioneer Museum, Tillamook, Oregon, October 20, 1959.*

Wilson Petrel off the California Coast.—On August 29, 1959, we identified a Wilson Petrel (*Oceanites oceanicus*) about two miles south of the Farallon Islands, California. There are few records of the species in California and for the west coast of North America. The first specimen was taken by R. H. Beck on Monterey Bay, August 24, 1910 (Grinnell, Pac. Coast Avif. No. 11, 1915:29) and the second by Loye Miller 25 miles west-northwest of Point Loma, San Diego County, August 31, 1935 (Miller, Condor, 38, 1936:13).

The bird remained around our boat for seven or eight minutes, and at times it approached within about 30 feet, when we had clear views of the characteristic yellow webs of the feet, which extended well beyond the end of the tail. The tail was square-ended, slightly rounded at the corners; the upper tail-coverts were pure white, without a dark center line; the remainder of the plumage was sooty-black, with the upper wing-coverts slightly grayer. The bird appeared about the size of a Fork-tailed Petrel (*Oceanodroma furcata*), which was in view at one time for comparison, but its wings were shorter and broader, and its flight was direct and deliberate, with slow, even wing-beats; it often settled on the water. On one occasion it dangled its legs and "walked" on the water in characteristic fashion.—I. C. T. NISBET, *Cambridge, England,* and R. G. MCCASKIE, *Tahoe City, California, October 21, 1959.*

Nesting Attempt by a Pair of Barn Swallows in Northern Alaska.—No species of bird wholly or even primarily dependent on flying insects for food has become established in the high arctic. This is not due to lack of opportunity to do so; for example, six of the eight species of swallows which occur on the North American mainland north of México have been recorded at Barrow, Alaska (Bailey, Colorado Mus. Nat. Hist. Popular Series, No. 8, 1948). The factors limiting the northward spread of these species are presumably connected with the scarcity of flying insect species in the arctic, their short season of activity, and the fact that periods of cold weather, even in the arctic summer, will keep insects inactive for days at a time. However, lack of proper nesting sites may also be limiting. In this light it is of interest to report an attempt by Barn Swallows (*Hirundo rustica*) to utilize an artificial site for nesting in an area north of the normal range of this species.

On June 17, 1959, two Barn Swallows were seen foraging over the tundra near the mouth of the Pitmegea River, Cape Sabine, Alaska. This species has not been recorded in two previous years of field work in this area (H. E. Childs, Jr., MS). On the following day one was seen near our tent, situated next to the river one mile from the coast. On the evening of June 19 two were seen there. From then until early July the pair was seen frequently. On June 22, courtship activity and attempted copulation were observed at our tent. On June 25 we found one member of the pair roosting in a deserted cabin at the mouth of the river. On July 1 a partly constructed nest, measuring 4½ by 2½ inches, was found built on the side of a beam in the cabin. No additional construction was done, and by the middle of July only one bird still remained in the area.

Barn Swallows were observed at two other localities in this general area in 1959. Maher recorded two at Cape Beaufort, 20 miles east of Cape Sabine, on June 27. On July 15, a male was collected by Childs at a locality seven miles inland along the Pitmegea River.

Bailey (*op. cit.*) indicates that nesting by Barn Swallows may occur, though rarely, in the Alaskan arctic. He cites a report by Charles Brower of a possible nesting at Barrow. Brower collected a female with three flying young of the year and suggested an abandoned sod igloo near the village as the probable nest site. The specimens have unfortunately been lost.

There are now two instances of Barn Swallows nesting or attempting to nest in the Alaskan arctic. Both times the birds sought a site which met their nesting requirements in an environment where these requirements were not found naturally. Such nesting attempts by vagrants lead to the colonization of new areas, an important event in the adaptation to climatic changes through geologic time.

These observations were made during field work on projects supported by the Arctic Institute of

North America and the Office of Naval Research.—HENRY E. CHILDS, JR., *School of Veterinary Medicine, University of California, Davis, California,* and WILLIAM J. MAHER, *Museum of Vertebrate Zoology, Berkeley, California, October 1, 1959.*

Rocky Mountain Race of the Williamson Sapsucker Wintering in California.—The winter occurrence in California of Williamson Sapsuckers of the Rocky Mountain race, *Sphyrapicus thyroideus nataliae,* was first reported in 1944 by Grinnell and Miller (Pac. Coast Avif. No. 27:236–237). At that time four specimens from the Providence Mountains, San Bernardino County, collected in January, one from near Susanville, Lassen County, also collected in January, and a September-taken specimen from 8 miles northeast of Hyampom, Trinity County, comprised the known records of *nataliae* in that state.

Comparison of a small-billed Williamson Sapsucker collected by the author in 1957 with other specimens in the Museum of Vertebrate Zoology revealed the existence in the collection of the museum of several further examples of *nataliae* from California. The following are the additional records: 3½ mi. E Weed, 5000 feet, Siskiyou County, male, December 21, 1934; Warner Creek, 6600 feet, Shasta County, male, September 24, 1923; Eagle Lake, Lassen County, female, October 14, 1923; Santa Cruz County, male, November 29, 1896; Sage Hen Creek, 6500 feet, Nevada County, female, November 12, 1950; and 2 mi. W Reyes Peak, 7000 feet, Pine Mountain, Ventura County, male, December 29, 1957.

These specimens all possess small bills. The two races overlap in bill length and width (Cowan, Condor, 40, 1938:128–129), but measurements do not adequately reveal the full extent of the difference in the bulk of the bills of the two forms. The bills of the specimens here listed are all well within the range of measurements of *nataliae* and are below the means for *S. t. thyroideus.* Careful visual comparison of overall bill sizes removes doubt as to their affinity to *nataliae.*

Thus, there are presently twelve records of the Rocky Mountain race wintering in California. The localities from which the various specimens have been taken are spread throughout the various mountain regions of the state, and the dates fall in the months from September through January. Nearly half of the twenty-five winter-taken specimens of Williamson Sapsuckers from California in the Museum of Vertebrate Zoology belong to *nataliae,* and at least two others should perhaps be assigned to that subspecies. These facts concerning numbers and distribution indicate a probable widespread migration of *nataliae* to the coniferous forests to the west of its breeding range.

The author wishes to express appreciation to Ned K. Johnson for aid and to Dr. Alden H. Miller for advice and loan of specimens.—RALPH J. RAITT, JR., *Department of Biology, New Mexico State University, University Park, New Mexico, December 28, 1959.*

NOTES AND NEWS

Members of the Cooper Society are again reminded of the dates of the Annual Meeting in Los Angeles in May of 1960. Scientific sessions are on Friday and Saturday, May 6 and 7. A tour of the Ray Thomas Aviary and a reception at the Los Angeles County Museum are scheduled for Thursday, May 5, in the afternoon and evening, and a field trip is planned for May 8.

A few copies of the January Condor have been found to be defective, with pages missing and duplication of others. Please send in faulty copies at once to Jack C. von Bloeker for replacement.

The editors call attention to the recent publication of three important books which, although not reviewed in detail here, are highly recommended to our readers. These are:

Wildlife of Mexico, The Game Birds and Mammals, by A. Starker Leopold, illustrated by Charles W. Schwartz (University of California Press, 1959, 568 pp., $12.50).

Life Histories of Central American Birds, Part II, by Alexander F. Skutch, illustrated by Don R. Eckelberry (Pacific Coast Avifauna No. 34, Cooper Ornithological Society, 1960, 593 pp., $15.00).

The Waterfowl of the World, Volume 3, by Jean Delacour, illustrated by Peter Scott (Country Life Ltd., London, 1959, 270 pp., approximately $17.60 at current exchange).

Notice is again given of the availability of $600 from the Josselyn Van Tyne Memorial Fund for aid in ornithological research. Any student of birds who has a special need for equipment, travel, assistance, or materials to further his research is invited to submit an application (10 duplicate copies) for a portion or all of the money available. This application should give a full description of the proposed research, the type of help that is required, when the money should be made available, the background and training of the applicant, and other pertinent information. The applications will be evaluated and rated by the Research Committee of the A.O.U. to determine how the funds will be allotted.

All applications for grants must be in the hands of the chairman not later than June 1, 1960.—S. Charles Kendeigh, *Chairman, Vivarium Building, University of Illinois, Wright and Healey Sts., Champaign, Illinois.*

From time to time the editors wish to draw to the attention of the readers of the Condor meaningful statements on conservation issues. Recently one of our members, Ian I. McMillan, has stated forthrightly some of his views and observations on conflicting procedures and programs that masquerade as conservation and desirable land use. We present parts of his letter to a worker concerned with agricultural extension services:

From where I sit I can look out on an expanse of good land that under applied research has taken a beating that only "applied research" could administer. We burn the cover from land that should remain in cover. We bulldoze down the trees to plant surplus crops on land that will not sustain cultivated crops. We dam the flood waters from denuded range to water more cattle so that the range can be further denuded. We supplement the forage on overgrazed ranges so that further ruin can be accomplished. On depleted, abused grain land we spray the weeds that grow on abused land, and we spray the grasshoppers that eat only the weeds. While normal amounts of rainfall bring floods of topsoil from cultivated, exposed slopes that should never have been cultivated, we spray the clouds in an effort to increase the rainfall and further accelerate the ruin, all under official guidance. We poison just about everything. We began a campaign a few years ago to eradicate the spotted alfalfa aphid that, if accomplished, would have also exterminated an insect fauna without which agriculture could not exist. This movement started, evidently, without even a juvenile concept of ecological principles. At public expense, we poison rodents on land placed in the Soil Bank at more public expense, as a measure to curtail the production of burdensome crop surplus. We poison the predators that prey on the same rodents.

I point this out to qualify, if possible, an objection to any more of the kind of "applied research" that has led to all this land-use travesty and fraud. Extension Services, more than any other forces, are responsible for this land-use picture. What they have done, however innocently, is to encourage and advise toward maximum, immediate, economic exploitation of the land without regard for end results. They have demonstrated and advocated only that which is most profitable economically. I have never noted any real concern for conservation or the future.

Through their influence and tutelage we have, on the local level, a leadership of prosperous ignoramuses.

Some of the questions that it is hoped will be answered through [your proposed study of rodent control] are questions that I had understood were officially answered before, or at least during, the vast control programs of the past four decades. Can this proposal be an admission by the boys who claimed to have all the answers that they really didn't know what they were doing? Why, after years of the wildest kind of control programs, purportedly based on scientific research, must we now start looking for the answers? And are we to rely now on the same school of thought that has previously been in error?

I certainly agree that we need research, but biased research is worse than none at all. And when economic interests such as the "progressive group of ranchers" mentioned in the proposal enter the picture, my eyebrows automatically elevate. I'm one of them and I know their outlook. They like your kind of research, ... and if they didn't I'm sure you wouldn't be proposing this project. I don't like the idea of one contending faction dominating the research on such a broad, controversial matter as rodent and predator control.

I am, however, somewhat curious as to the complete origin of this proposal. As you will agree, this kind of a project can be as much a human relations vehicle as anything else. It would be a major catastrophe in my opinion, to have it contribute to the further spread of the poison-burn-spray epidemic that is already rampant throughout California.

Programs of the Southern Division of the Cooper Society in 1959 and early 1960 have included Dr. William Beckwith, Department of Psychology, University of California, Los Angeles, speaking on "The Study of Imprinting," on May 26; Dr. Andrew Starrett, Department of Biology, University of Southern California, on "The Biogeography of Costa Rica," on September 26; Kenneth Stager of the Los Angeles County Museum, on "The Machris-Los Angeles Museum Expedition to India," on October 27; a film by Mr. Charles W. Schwartz of the Missouri Conservation Commission, on "The Life History of the Mourning Dove," on November 28; and Dr. Walter P. Taylor, presenting "Travel Notes of a Naturalist," on January 27.

Northern Division programs since November, 1959, have presented Mrs. Betsey D. Cutler, Department of Biology, San Francisco State College, speaking on "Birds of West Bengal," on November 5; George E. Lawrence, Bakersfield College, on "Vertebrate Survival in Brush Fires," on December 3; Dr. Robert C. Miller, Director of the California Academy of Sciences, on the question "Do Birds Perceive Radar?" on January 7; and Gordon H. Orians, Museum of Vertebrate Zoology, on "Spring and Fall Breeding in the Tricolored Blackbird," on February 4.

Recently the extensive private collection of birds of the late Ralph Ellis, Jr., has been given to the Museum of Vertebrate Zoology at Berkeley through the generosity of the former Mrs. Ellis in pursuance of the intent of Mr. Ellis. For many years the collection has been on deposit at the Museum for the use of research workers there.

For Sale, Exchange, and Want Column—Each member of the Cooper Society is entitled to one short advertising notice in any issue of the Condor free. Notices of over 3 lines will be charged for at the rate of 25 cents per line. Send advertising copy to Jack C. von Bloeker, Jr., Los Angeles City College, 855 N. Vermont Ave., Los Angeles 29, California.

WANTED—Forty-seventh Christmas Bird Count (Audubon Field Notes, vol. 1, No. 2, March, 1947). Needed to complete my file.—C. STUART HOUSTON, *Box 278, Yorkton, Saskatchewan, Canada.*

FOR SALE—A limited number of "Birds of the Southwest," by Charles Aiken, Colorado College Studies, No. 23, 1937, $1.00 postpaid.—RICHARD G. BEIDLEMAN, *Colorado College, Colorado Springs, Colo.*

FOR EXCHANGE—Nuttall Bulletin, vols. 3, 6 and 7, and/or 8, for the Auk, vol. 3, 1886.—DAVID K. WETHERBEE, *Stockbridge Hall, Univ. Massachusetts, Amherst, Mass.*

FOR SALE—Original and famous Nieland tree identification wheels. Covers 53 trees of Central and Eastern U. S., 17 facts about each. Use in field or classroom. $1.25 ea., postpaid anywhere in U. S.—W. SHAUGHNESSY, *R.F.D. No. 2, Hamilton, Ga.*

FOR SALE OR TRADE—"Arizona Flora," by T. H. Kearney and R. H. Peebles, 1951, in excellent condition, $7.00.—RONALD T. REUTHER, *Cleveland Zoological Park, Cleveland 9, Ohio.*

FOR SALE—The Condor, vols. 36–61, 1934–59; also Pac. Coast Avifauna No. 28 (4th 10-year index to the Condor, vols. 31–40, 1929–38) and No. 30 (5th 10-year index to the Condor, vols. 41–50, 1939–48). Make offer.—MRS. C. S. DEUPREY, *817 University St., Healdsburg, Calif.*

FOR SALE—Write for complete details and specifications on Specimen Case no. 112, designed by the University of California. Size 27″ × 44″ × 42″ priced at $199.00, F.O.B. Escondido, Calif.—CHAPPELL'S HOUSE OF WOODCRAFT, *P. O. Box 1085, Escondido, Calif.*

FOR SALE—Books on birds and natural history. Write for price-list.—MRS. JOHN Q. BURCH, *4206 Halldale Ave., Los Angeles 62, Calif.*

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WANTED—Bull., Cooper Ornith. Club, vol. 1, nos. 3–4; Condor, vol. 2, no. 6, and vol. 3, no. 2; will buy any one, two, three, or all four copies; needed to complete my file.—JACK C. VON BLOEKER, JR., *Los Angeles City College, 855 N. Vermont Ave., Los Angeles 29, Calif.*

LIFE HISTORIES OF CENTRAL AMERICAN BIRDS

Part II

Families Vireonidae, Turdidae, Sylviidae, Troglodytidae, Paridae, Corvidae, Hirundinidae, and Tyrannidae

By ALEXANDER F. SKUTCH

Illustrated by Don R. Eckelberry

The Cooper Ornithological Society announces the publication of Part II of the Life Histories of Central American Birds as Pacific Coast Avifauna No. 34.

This volume extends Dr. Skutch's important and fascinating record of his life-time study of the natural history of tropical birds. His writings have won acclaim by award of the Brewster Medal of the American Ornithologists' Union and they have been supported by a fellowship of the Guggenheim Foundation. Dr. Skutch not only has the ability to observe and to listen, but he also possesses a flair for writing so that his accounts are a pleasure to read. Part I of his work was published by the Society in 1954 as Avifauna No. 31.

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